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Genetics of behavioural adaptation of livestock to farming conditions

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Behavioural adaptation of farm animals to environmental changes contributes to high levels of production under a wide range of farming conditions, from highly controlled indoor systems to harsh outdoor systems. The genetic variation in livestock behaviour is considerable. Animals and genotypes with a larger behavioural capacity for adaptation may cope more readily with varying farming conditions than those with a lower capacity for adaptation. This capacity should be exploited when the aim is to use a limited number of species extensively across the world. The genetics of behavioural traits is understood to some extent, but it is seldom accounted for in breeding programmes. This review summarizes the estimates of genetic parameters for behavioural traits in cattle, pigs, poultry and fish. On the basis of the major studies performed in the last two decades, we focus the review on traits of common interest in the four species. These concern the behavioural responses to both acute and chronic stressors in the physical environment (feed, temperature, etc.) and those in the social environment (other group members, progeny, humans). The genetic strategies used to improve the behavioural capacity for adaptation of animals differ between species. There is a greater emphasis on responses to acute environmental stress in fish and birds, and on responses to chronic social stress in mammals.

Keywords: behavioural genetics, fish, cattle, pig, poultry

Implications

At a time of rapid change in animal genetics, with the development of genome-wide analyses with potential applications in the improvement of traits related to livestock welfare, the authors were interested in reviewing the knowledge obtained so far on the quantitative genetics of behavioural traits in four main livestock productions: cattle, pigs, poultry and fish. The mixing of complementary information from these different livestock productions gives arguments for the integration of behaviour into selective breeding programmes.

Introduction

Today, the breeding of livestock species is moving towards the complementary use of local breeds and high-production genotypes to ensure stable production in a wide range of climates and production systems (Food and Agricultural Organization (FAO), 2006), in an attempt to overcome the worldwide nutritional and ecological challenges of the 21st century

(Knap, 2005; Ten Napel *et al.*, 2006). The adaptation of animals to the stress elicited by their physical and social environments is one of the first functions under consideration when the objective is to increase production in diversified breeding systems. At all times, animals respond behaviourally to challenges in order to maintain homeostasis (Koolhaas *et al.*, 1997). Density, food allowance, housing conditions, that is, more or less extensive husbandry and more or less close relationships with other group members, progeny and humans, are among the many factors mediating the behavioural strategies of an animal. High-production livestock genotypes are exported more and more frequently to South America and other tropical countries. Their capacity for adaptation to hot conditions will have a large role to play in their survival, especially when they are sent to countries with both a warmer climate and a lower feed allowance than their country of origin.

Adaptability is defined as the degree to which animals adapt to different environments (Barker, 2009) and is related to functional traits (reproduction and health) that preserve or enhance fitness, that is, survival. In general, functional traits show low heritability and depend more on genotype–environment interactions than production traits (Frankham, 2009). As a consequence, their improvement through artificial

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selection is inherently more difficult than that of production traits. The behaviour of an animal (e.g. feeding behaviour, maternal behaviour) contributes to its fitness and can be used as a welfare indicator because its modification may reveal both the existence of stressors and a lack of adaptation to these stressors. Through behavioural adaptation, the animal adjusts its behaviour to favour its fitness in the local environment. Resource allocation theory states that when too much energy is allocated to production, an animal will be unable to cope successfully with environmental changes and/or novel pressures of selection (Beilharz *et al.*, 1993; Schütz *et al.*, 2004). More robust animals are those that maintain performance despite environmental changes (Knap, 2005).

In recent decades, a combination of genetic selection for production traits and changes in production systems has induced a rise in the prevalence of behavioural disorders (Rauw *et al.*, 1998; Rauw, 2007). Animals may even develop redirected behaviours, including stereotypes, when stressors act intensively (Dantzer and Mormède, 1983; Bizeray *et al.*, 2000). Livestock management can expose animals to multiple stressors that may cause poor welfare and possibly production loss. Genetic research designs are developed to allow the investigation of behavioural genetic strategies that can be used to reduce the sensitivity of an animal to its physical environment, to limit excessive fear of humans and to eliminate social disorders that environmental modifications cannot resolve. Livestock face acute stressors when they endure a sudden, even if temporary, change of environment or a perturbation within their environment. They may also face chronic stressors when the aversive perturbation either occurs for a long continuous period of time or is temporary but repeated over time. Chronic stressors may have long-term effects on fitness.

The review was performed to investigate whether trends can be observed, across the four major livestock productions: cattle, pigs, poultry and fish, in the genetic capacity of animals for behavioural adaptation to acute and chronic changes in their physical and social environments. Estimates of heritability and genetic correlations between behaviour and production traits will be summarized. The results from experiments of divergent selection for behaviour will also be presented. From this information, we will evaluate whether or not genetic strategies that are common to several species can be used to improve the behavioural adaptation of livestock to farming conditions.

On-farm assessment of behavioural adaptation in livestock

Impact of domestication and selective breeding on livestock behaviour

Previous species-specific reviews on this topic have described the high degree of genetic variation in livestock behaviour (cattle: Boissy *et al.*, 2002; pig: Mercat and Mormède, 2002; poultry: Mignon-Grasteau and Faure, 2002; fish: Vandeputte and Prunet, 2002). Animal behaviour and welfare are affected by domestication and selective breeding in different ways, according to the number of traits targeted. In addition, the

pressures of selection on different traits may interact and balance each other in selective programmes, so that the consequent modifications in behaviour may sometimes be limited.

For domestication, species and animals have been chosen for their relatively low sensitivity to the stress of confinement and for social skills that enable reproduction even when the population density is high (Mignon-Grasteau *et al.*, 2005). Some features of domestication, if extreme, may decrease the capacity of an animal for adaptation. Gregariousness was boosted strongly in laying hens, and as a result these animals show difficulties in coping with social changes (Väisänen *et al.*, 2005). Domesticated populations have diverged from their wild ancestors with respect to a decreased level of activity, as observed in poultry (Jensen *et al.*, 2005; Branciaro *et al.*, 2009) and pigs (Bergeron *et al.*, 1996). Fish species for which domestication is at a relatively early stage will shed new light on the topic of this review in comparison with other species. As a result of poikilothermy and because they are raised in fluctuating environments, fish are highly sensitive to stressors in the physical environment. They allocate much energy to maintaining homeostatic balance when they face environmental perturbations such as changes in the water quality, which occur frequently. This process of coping starts at the fingerling stage, when the eggs are exported to countries and regions with greatly different production ecology from that of the original home of the fish (with respect to water quality, management and pathogens). It appears that the domestication of fish reduces their sensitivity to stressors. Hatchery-reared fish generally exhibit different distribution in the water column, higher boldness and a higher risk of predation when foraging than wild fish (trout: Johnsson and Abrahams, 1991; Lepage *et al.*, 2000; Alvarez and Nicieza, 2003; Sundstrom *et al.*, 2004; salmon: Einum and Fleming, 1997; Johnsson *et al.*, 2001).

Intensive genetic selection for production causes significant changes in a limited number of traits (e.g. muscle growth, milk yield and egg production). As side-effects, some harmful morphological changes can be observed, and physiological and behavioural disorders may emerge (Rauw *et al.*, 1998; Rauw, 2007). Intensive selection for a few traits tends to increase sensitivity to stressors in the physical environment. This was shown by Väisänen and Jensen (2003) and Huff *et al.* (2007) in the males of modern breeds of poultry, which display greater difficulties in adjusting to a novel environment than their wild ancestors. However, the main alterations observed relate to the global activity of animals and their social behaviour.

Pigs seem to be the most physically sound, whereas both broiler chickens and dairy cows suffer from leg weakness, with the result that disorders of locomotion are reported in these species (Le Bihan Duval *et al.*, 1996; Løvendahl and Munksgaard, 2005) and morphological changes can also develop in Atlantic salmon (Gjerde *et al.*, 2005). Livestock species show increased appetite and feeding activity, which is required to sustain their increased genetic potential for production (e.g. dairy cattle: Dado and Allen, 1994; brown trout: Mambrini *et al.*, 2004). Pure line broilers illustrate an

extreme case in which selection has increased appetite and growth so greatly that the feed supplied to the breeding animals has to be restricted severely in order to maintain their reproductive potential (Beaumont *et al.*, 2010).

In poultry, there is evidence that chronic stressors have made modern laying hens more fearful of humans than their ancestors (Jones *et al.*, 1988). Selection for early sexual maturity and egg production in hens has increased aggression and social dominance, which leads to higher levels of feather pecking and cannibalism in a large variety of environments (Craig *et al.*, 1975; Kjaer and Mench, 2003). Beak trimming, which was introduced to reduce the prevalence of these behavioural disorders, now causes welfare concern because it inflicts pain in both the short and the long term (Gentle *et al.*, 1997). In fish, an increase in aggression is often feared because the recent selection for growth, which was applied to high-density stocks, has been successful. In pigs and cattle, there is no clear evidence that selection for growth has had a negative influence on the aggression of animals towards other group members, progeny or humans.

Surveys on the genetics of behaviour in livestock science

Literature surveys on the genetics of behaviour have emerged only recently, with most studies starting at the end of the 20th century. Over the last two decades, publications relating to cattle and pigs were more numerous, but genetic studies accounted for a lower proportion (3.5% and 7.5%, respectively) than in studies on poultry and fish (~10% in the two livestock productions over the 2001 to 2011 period; Figure 1). In human society, genetic selection of livestock is a controversial practice. On the grounds of the evident physical modifications and more subtle changes in homeostasis that may lead to pathology, genetic selection is sometimes claimed to lead to deterioration in animal welfare (Grandin and Deesing, 1998; Beaumont *et al.*, 2010; Oltenacu and Broom, 2010). On the other hand, maternal behaviour that is beneficial to animal welfare can be detrimental to the safety of the handler. In addition, modern poultry may no longer be adapted to large spaces because their drive for foraging, and their motivation to use space and general activity have been decreased by genetic selection (Branciarri *et al.*, 2009). Welfare is dependent on the animal's perception of its environment and its reaction to environmental stimuli (Dantzer and Mormède, 1983), which may evolve with selection. Herein, we use behaviour as an indicator of welfare, assuming that this external response is well correlated to the inner state of the animal. Dawkins (2004) presented the many advantages of using behaviour in this context, because its measurement is the result of the animal's decision-making processes and, ultimately, it is the expression of the animal's motivational affective state.

Studies have targeted hotspot issues that are species specific. A good relationship between livestock and humans is a priority in large mammals. In pigs, there has also been increased interest in sociality because welfare policies recommend raising these animals in groups. In fish and poultry, experimental approaches that include a greater number of traits can be implemented.

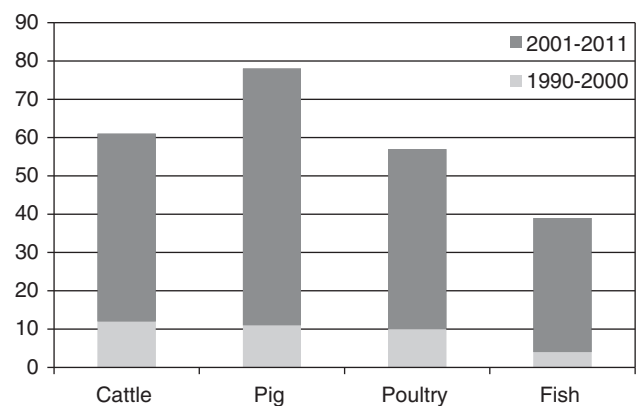


Figure 1 Scientific publications dedicated to the genetics of behaviour in cattle, pigs, poultry and fish (Source: Web of Science database <http://apps.webofknowledge.com/>; keywords: (heritability or QTL) and behaviour and (cattle or poultry or pig or fish) – accessed 15/02/2012). QTL = quantitative trait loci.

In this review, we will refer mainly to estimates of heritability obtained from the statistical analysis of phenotypes collected either from selection nucleus populations or from experimental lines obtained by divergent selection for a behavioural trait of interest. The emergence of genomic tools has shed light on novel methodologies of investigation and selection in livestock, with the possibility of targeting genes of interest directly. The detection of quantitative trait loci (QTL) in experimental populations is a powerful approach to understanding the genetics of behavioural adaptation to farming conditions. However, the proportion of QTL detected for behavioural traits is low (<3% in the four livestock productions studied, <http://www.animalgenome.org/cgi-bin/QTLdb/index>).

Behavioural tests used to assess the genetics of adaptation

Tests developed in model species such as laboratory mice can be used for quantitative genetic studies in livestock (Table 1) because they are reasonably meaningful for a wide range of species. However, readers should be aware that different motivational systems and cognitive abilities exist in different species (Dantzer, 2001), so that there are some limits to the extrapolation of results across species. The tests are usually intended to elicit a response in the animal either to its physical environment or, as independently as possible, to its social environment. Response to an acute stress can be assessed in isolated animals placed in an unfamiliar environment or in presence of other group members. The open-field test, which investigates the animal's reaction to a non-social situation, is a basic test that is common to the four livestock productions. Its principle is to induce a conflict between aversion and voluntary exploration of a novel environment. Locomotion and exploration are good indicators of adaptation to change, if they decrease as fast as the animal adjusts to novelty. However, some animals may react with a state of apparent tetany when they enter the test environment. This observation illustrates that a large range of variation in the behavioural response to challenges exists among families, populations and species. This remark is valid

Table 1 Tests used for the genetic assessment of the behavioural response of animals to stressors in the physical and social environments of production in cattle, pig, poultry and fish

Test and description ^a	Cattle D: Dairy; B: Beef	Pig	Poultry H: laying Hen; B: Broiler; Q: Quail; T: Turkey	Fish S: Salmon; T: Trout; Z: Zebra
Response to the physical environment				
NO RESTRAINT – ISOLATED OPEN-FIELD TEST: reaction when isolated from group members	D: after removal of the group from home pen, one animal is moved back with cattle present in the adjacent pen [1] ^b	Pig into a van with floor divided by painted lines into several sections, with wood shavings spread over [3]	H: in a room kept dark until start [4, 5] Q: in a box with observer hidden [6] T: in a pen with visual contact with turkeys but observer hidden [7]*	T: 1 week after isolation from the stock tank to a glass tank screened from visual disturbance [8]*; ARENA TEST in a tank including a shelter place, an open area and a T-MAZE TEST [9]*
NO RESTRAINT – ISOLATED NOVEL OBJECT TEST: object unfamiliar added in a open field			H: a red and white fishing float placed into the trough [5]	T: orange frustum-shaped bung and bipyramidal construct is added [8]*
NO RESTRAINT – GROUP NOVEL OBJECT TEST	B: scoring in a field at the ranch [2]	A black bucket descended from the ceiling in the middle of the home pen [10]	Q: a multi-colored cylinder placed into the cage gently by hand [11]	
Response to the social environment				
Response to other group members SEARCH FOR CONTACT – ISOLATED SOCIAL-REINSTATEMENT TEST: motivation to join group members			Q: in a treadmill [12] H: in circular pen with zones defined by distance and visibility of other hens [13] T: T-MAZE TEST: turkeys at end of an arm and a mirror at end of the T [7]*	
DYADIC ENCOUNTER – ISOLATED RESIDENT-INTRUDER TEST: between unfamiliar animals in a novel environment AGGRESSION – GROUP: at higher density than usual condition	B: DOMINANCE TEST in tournaments [14]	A pig of same sex placed with the resident pig until one pig attack the other [10] After mixing of pregnant sows in a testing arena [18]	H: Mirror test [13] H: [4]	T: a fish is added in the arena [15, 16] S: Mirror test mirror placed over the back of the aquarium [17]* T: CONFINEMENT TEST: 3 h in groups once monthly [19]
Response of dam to offspring SOCIAL CONTACT MAINTAINED PROGENY-HANDLING TEST	B: during catching, removing and earmarking of the calf [20]	Handler picks up a piglet in the pen and squeeze it or plays the tape record of a screaming piglet [SCREAM TEST 21]		
SOCIAL CONTACT DISRUPTED SEPARATION TEST		When piglets are weighed [22]		

Table 1 Continued

Test and description ^a	Cattle D: Dairy; B: Beef	Pig	Poultry H: laying Hen; B: Broiler; Q: Quail; T: Turkey	Fish S: Salmon; T: Trout; Z: Zebra
Response to human or predator				
NO RESTRAINT ACCEPTANCE OF HUMAN: voluntary approach of the animal or human approach	B: GROUP: human approach at the feeder [1]	GROUP: a human, who the pigs are unfamiliar with, enters the pen and stands motionless in the pen [10]		S: ISOLATED: a simulated predator added in the test tank (trout) equipped with a tunnel with refuge [23]*
MODERATE RESTRAINT – GROUP HANDLING TEST: separation attempt from the flock	B: handler attempt to separate one animal from the group into a smaller arena [24]		H: RESTRAINT TEST* a rope is tied to the left leg of the bird and the other end of the rope to a pole fixed to the floor [5]	
HIGH RESTRAINT – ISOLATED RESTRAINT TEST: reaction of the animal to a restraint (by device or human constraints)	B: CHUTE TEST: while restrained in the head gate [27] B: IN-SCALE TEST: on a weighing scale [25, 26]	BACK TEST: pig placed gently onto its back and restrained [10] IN-SCALE TEST: on weighing scale [28]	Q: BACK TEST: quail placed on its back and restrained with a hand on sternum and the other cupping the head [12]	
ESCAPE AFTER HIGH RESTRAINT – ISOLATED: exit or attempt to exit an unfamiliar environment	B: FLIGHT SPEED TEST: cover of a fixed distance while exiting a confined area [29]	FLIGHT SPEED TEST: cover of a fixed distance between light sensitive diodes at a weighing scale exit [30]	Q + H: TONIC IMMOBILITY TEST: after back-test, the observer retreats [5, 31] T*: GROUP when caught and moved to a novel environment [7]	

^aTest is defined according to the level of restraint applied by the experimenter on the animal, whether the test is performed on animals isolated from the rearing group (ISOLATED) or on animals kept among the rearing group (GROUP) and the name of the test (in capital). When the experimental condition is specific, precisions on the test are given in the cell of the species.

^bGenetic references associated, describing the test or referring to it in a previous publication: [1] Gutierrez-Gil *et al.* (2008); [2] Silva *et al.* (2006); [3] Désautés *et al.* (2002); [4] Rodenburg *et al.* (2004); [5] Schütz *et al.* (2004); [6] Mignon-Grasteau *et al.* (2003); [7] Huff *et al.* (2007); [8] Thomson *et al.* (2011); [9] Ruiz-Gomez *et al.* (2011); [10] Velie *et al.* (2009); [11] Schweitzer and Arnould (2010); [12] Mills and Faure (1991); [13] Wirén and Jensen (2010); [14] Sartori and Mantovani (2010); [15] Øverli *et al.* (2002); [16] Pottinger and Carrick (1999); [17] Vollestad and Quinn (2003); [18] Lovendahl *et al.* (2005); [19] Øverli *et al.* (2006); [20] Hoppe *et al.* (2008); [21] Grandinson *et al.* (2003); [22] Hellbrügge *et al.* (2008); [23] Einum and Fleming (1997); [24] Gauly *et al.* (2001); [25] Morris *et al.* (1994); [26] Schmutz *et al.* (2001); [27] Hoppe *et al.* (2010); [28] Holl *et al.* (2010); [29] Burrow (1997); [30] Crump *et al.* (2005); [31] Satterlee *et al.* (1993).

*Tests used for breed comparison only.

for most recorded behaviours: they show phenotypic variation in relation to different coping strategies that distinguish between animals with a fight–flight response and those with a freeze–hide response (Koolhaas *et al.*, 1997). Accordingly, the novel object test can be used to differentiate between shy and bold animals.

The behavioural response depends on conditional factors. It may be relatively less intense when the test is performed in the home environment rather than in a novel environment, when a period of adaptation to change precedes recording, when other group members are present in the neighbourhood or when humans are not visible or remain at a distance. Conversely, a relatively strong response is elicited when the change is made more suddenly (e.g. switching on the light, forceful handling to move the animal to the experimental location).

Different tests have been developed to account for different social contexts and various levels of restraint in beef cattle. These tests have been modified more recently for use in pigs. The interference from humans is variable: the animals may be relatively unrestrained, given more room to allow the expression of motivational processes among the rearing group, or tightly restrained, so that both sources of social interaction (humans and other group members) can have confounding effects on reactivity. The docility test, the output of which depends on the animal's voluntary cooperation, elicits a less intense response than the on-scale test or the chute test.

Single-trait assessment of behaviour is influenced strongly by the environment and past experience of the animal (Forkman *et al.*, 2007). Moreover, interactions between the physical and the social environment may affect the behavioural response in all the tests that are described in the review. Experimental designs often target several behavioural components; this results in a non-specific response but gives a clear advantage in the assessment of the animal's personality. Even if the use of behavioural tests is generalized to different species, the correlation between reactivity in an experimental environment and reactivity under commercial farming conditions remains generally unknown. This point should be clarified before selection is considered on the basis of the behaviour elicited by a test situation. Furthermore, there is an obvious lack of standardization in test situations (e.g. ground surface, luminosity, temperature) that can strongly affect the estimation of genetic parameters for behavioural traits. Despite the evidence that the environment can have a considerable influence on behaviour (Grandinson *et al.*, 2003), few experiments have been carried out to estimate the interaction between genotype and environment with regard to behavioural traits.

Genetics of the behavioural response to changes in the physical environment

Estimates of the heritability of the behavioural responses to acute and chronic changes in the physical environment are presented in Table 2. Genetic correlations with production traits are shown in Table 3.

Response to acute stressors

The genetic variation in the response to an open field or novel object has been investigated mainly in poultry. Latency to move and locomotion in the open field show highest heritability in broilers and hens (Table 2). Exploration of a novel object is moderately heritable in broilers, and a few QTL were identified that correlated with a QTL for growth on Golgi-localized, gamma-ear-containing, Arf-binding protein 1 (GGA1) in hens (van der Poel *et al.* in Buitenhuis *et al.*, 2005). Breed variation in excitability in a novel environment also exists in pigs (Shea-Moore, 1998). The gene associated with the porcine stress syndrome impairs the capacity for adaptation to stressors. Therefore, nn pigs have been eradicated from various populations. Behavioural differences have also been found among other genotypes: pigs with the genotype Nn at the locus for the ryanodine receptor gene RYR(1) are less active than NN pigs in the open-field test (Fabrega *et al.*, 2004). Désautés *et al.* (2002) found different QTL in pigs to be associated with locomotion on SSC1, or with exploration on SSC8. In beef cattle, locomotion in open field shows moderate heritability and is correlated unfavourably with growth and milk production (Phocas *et al.*, 2006). In dairy cattle, QTL associated with vocalization and locomotion when isolated from the herd are located mainly on BTA16 and BTA19 (Gutierrez-Gil *et al.*, 2008). Using different strains of zebra fish, several QTL for boldness when facing novel objects have been highlighted. In addition, a genomic region that influences anti-predator behaviour shows some co-location with QTL for resistance to heat shock and growth capacity in water of varying salinity (Wright *et al.*, 2006).

Response to chronic stressors

When exposed to chronic stressors, the reactions of animals can be more durable. For example, exposure to high ambient temperature has a direct impact on animal survival and health, and is associated with modification in locomotion and feeding activities. These behavioural responses indicate the level of heat tolerance of an animal. Thermal stress has a significant impact on feed intake and feed efficiency in poultry (Chen *et al.*, 2008).

Global activity. Global activity is assessed by postural changes and locomotion, with low to moderate heritability reported in the three terrestrial species (min $h^2 = 0.05$; max $h^2 = 0.35$). In pigs, lameness is more heritable than locomotion ($h^2 < 0.10$). Conversely, locomotion shows breed variation in genetic estimates for dairy cattle, and high heritability was observed (Boelling *et al.*, 2007). Moreover, locomotion is a good indicator of health because it is genetically correlated with the presence of claw disorders ($r_g > -0.40$; Laursen *et al.*, 2009). On the basis of the results from a study of divergent selection for growth, Nestor *et al.* (2008) showed alteration in walking ability in turkeys. Walking ability was moderately heritable and correlated favourably with survival ($r_g > 0.60$) and with hip and leg strength ($r_g > 0.85$; Quinton *et al.*, 2011). At the genetic

Table 2 Estimates of heritability (h^2) and QTL identification* for the behavioural response of animals to stressors in the physical and social environments of production in cattle, pig, poultry and fish

Test situation	Stress applied	Type of behaviour	Cattle D: Dairy; B: Beef	Pig	Poultry H: Laying Hen; B: Broiler; Q: Quail; T: Turkey	Fish S: Salmon; T: Trout; Z: Zebra
Response to the physical environment						
OPEN-FIELD ACTIVITY	ACUTE	LATENCY TO MOVE	D: standing alert QTL 5 [1]		H: latency to move h^2 0.20/0.45 [2] B: latency to move h^2 0.04 [3] B: latency to move QTL 3 [4] 1 [7]	
		LOCOMOTION	B: running time h^2 0.23 [5] D: locomotion index QTL 6 [1] B: N escape attempts h^2 0.09 [5]	locomotion time QTL 1 [6]	B: locomotion activity h^2 0.36 [3] H: steps h^2 0.49 [2] H: flying frequency h^2 0.04/0.20 [2] B: head flicks QTL 3 [7]	
		EXPLORATION		Rooting and sniffing time QTL 1 [6] Novel object h^2 0 [9]	H: ground pecking QTL 2 [8] B: novel object h^2 0.18 [10] B: novel object QTL 1 [8]	Z: novel object QTL 6 [11]
ON-FARM ACTIVITY	CHRONIC	VOCALIZATION	D: vocalizations QTL 11 [1] D: lying time h^2 0.01 [12] D: standing time h^2 0.14 to 0.23 [13]		H: calls h^2 0.09/0.32 [2] H: calls QTL 5 [4]	
		POSITION		Sitting frequency h^2 0.43 [14] Lying time QTL 3 [13] Drinking time QTL 6 [15]	H: sitting or standing time h^2 0.33 [16] H: sitting activity h^2 0.83 [17] Q: dust-bathing h^2 0.15 to 0.30 [15]	
		LOCOMOTION	B: continuous mobility h^2 0.14 [18] D: step/gait h^2 0.05 to 0.10 [19, 20] D: lameness h^2 0.01 to 0.22 [20, 24]	Leg action h^2 0.06 to 0.08 [21, 22] Leg action QTL 7 8 [13] Lameness h^2 0.01 to 0.40 [25, 26]	T: walking ability 0.25 [23]	
		EXPLORATION DAILY FEEDING	B: time h^2 0.28 to 0.36 [27, 28] D: time h^2 0.14 [12] B: frequency h^2 0.38 [27] B: rate h^2 0.51 [28]	Rooting and sniffing time QTL 2 [13] Time h^2 0.36 to 0.44 [28, 29] QTL 8 [13] Frequency h^2 0.43 [28, 29] QTL 4/2 [31, 33] Rate h^2 0.44/0.50 [29, 34]	H: ground pecking h^2 0.13/0.30 [3] B: time h^2 0.30 to 0.36 [32] B: frequency h^2 0.54 to 0.58 [32] B: contra-freeloading QTL 7 [7]	
Response to the social environment						
Response to other group members						
SOCIAL MOTIVATION	ACUTE	SEARCH CONTACT			Q: distance covered h^2 0.22 to 0.66 [35] Q: distance covered QTL 1 [7]	Z: shoaling h^2 0.40 [36] Z: shoaling QTL 3 [11]
DYADIC ENCOUNTER	ACUTE	DOMINANCE	B: score h^2 0.20 to 0.36 [18, 37]	Latency to attack h^2 0 [9] Dominance score h^2 0.12 [9]		S: dominance index h^2 0.70 [38]

Table 2 Continued

Test situation	Stress applied	Type of behaviour	Cattle D: Dairy; B: Beef	Pig	Poultry H: Laying Hen; B: Broiler; Q: Quail; T: Turkey	Fish S: Salmon; T: Trout; Z: Zebra
ON-FARM AGGRESSION [GROUP]	ACUTE	AGGRESSION		Female delivery h^2 0.09 to 0.32 [41, 42] Female receipt h^2 0.02 [42] Bullying time h^2 0.31 [39] Fighting time h^2 0.42 [39] Bullying receipt h^2 0.08 [39]	B: receipt h^2 0.25 [10] B: delivery h^2 0.19 [10] H: receipt h^2 0.02 [2] H: delivery h^2 0.18 [43] H: gentle delivery h^2 0.08 to 0.18 [2, 44] H: gentle delivery QTL 3 [46] H: severe delivery h^2 0.02 to 0.14 [2, 44] H: severe delivery QTL 1 [46] H: pecking index h^2 0.65 [45]	S: fighting time h^2 0.25 [40]
ON-FARM AGGRESSION [GROUP]	CHRONIC	AGGRESSION		Female social rank h^2 0 [47] Male social rank h^2 0.47 [47] Tail-biting h^2 0 to 0.27 [48]		
Response of dam to progeny PROGENY REMOVAL PROGENY	ACUTE ACUTE	REACTIVITY AGGRESSION	B: reactivity h^2 0.32 to 0.36 [5, 50]	Reactivity h^2 0.08 to 0.16 [44, 52, 53] Aggression h^2 0.08 [52] crushing h^2 0.06 [54] Cannibalism h^2 0.20 to 0.90 [55, 56] Cannibalism QTL 7 [57, 58]		
ON-FARM OBSERVATION	CHRONIC	MATERNAL ABILITY	B: protection h^2 0.14 to 0.42 [51] B: protection score h^2 0.09 [49]	Maternal score h^2 0.02 to 0.08 [53]	H: egg incubation QTL 3 [59]	
Response to human or predator ON-FARM OBSERVATION	ACUTE CHRONIC	APPROACH APPROACH	D: flight distance QTL 4 [1]	Voluntary if isolated h^2 0.38 [60] Voluntary if in group h^2 0/0.03 [10] Aggressive score h^2 0.11 [53] Protest to move score h^2 0/0.22 [53] Good sow score h^2 0.04 [53]		
HANDLING SEPARATION	ACUTE	LOCOMOTION ESCAPE DOCILITY	B: running time h^2 0.21 [5] B: N attempts h^2 0.26 [5] B: docility score h^2 0.11 to 0.64 [61] B: docility index h^2 0.18 [5] B: aggression index h^2 0.20 [5] B: ease handling QTL 9 [62]			

Table 2 Continued

Test situation	Stress applied	Type of behaviour	Cattle	Pig	Poultry	Fish
			D: Dairy; B: Beef		H: Laying Hen; B: Broiler; Q: Quail; T: Turkey	S: Salmon; T: Trout; Z: Zebra
HIGH-RESTRAINT	ACUTE	LOCOMOTION	B: on-scale mobility h^2 0.14 to 0.36 [64] B: mobility QTL 6 [64] B: Chute score h^2 0.11 to 0.33 [63]	On-scale activity score h^2 0.23/0.30 [65]	H: restraint with rope QTL 5 [7]	
		IMMOBILITY		Back-test time h^2 0.49 [9]	H: immobility time h^2 0.28 [66] Q: immobility time h^2 0.12 to 0.23 [62] Q: immobility time QTL 1 [67]	
		ESCAPE	B: No. of attempts h^2 0 to 0.05 [61]	No. of attempts h^2 0.53 [9]	Q: No. of attempts QTL 1 [67, 68] H: No. of attempts QTL 2 [7]	
ON-FARM OBSERVATION	ACUTE	FLYING	B: flying time h^2 0.49 [27] B: speed score h^2 0.11 to 0.44 [73, 63] D: speed 0.10 to 0.29 [70, 71, 72] D: speed QTL 5 [72] D: docility h^2 0.07 [72] D: nervousity QTL 5 [72]	Flying time h^2 0.14 to 0.17 [69]		
		MILKING				

QTL = quantitative trait loci.

*The number of different chromosomes where QTL region(s) were detected is specified.

References: [1] Gutierrez-Gil *et al.* (2008); [2] Rodenburg *et al.* (2004); [3] Mignon-Grasteau and Faure (2002); [4] Buitenhuis *et al.* (2004); [5] Phocas *et al.* (2006); [6] Désautés *et al.* (2002); [7] Schütz *et al.* (2004); [8] Buitenhuis *et al.* (2005); [9] Velie *et al.* (2009); [10] Bessei (1995); [11] Wright *et al.* (2006); [12] Løvendahl and Munksgaard (2005); [13] Reiner *et al.* (2009); [14] McGlone *et al.* (1991); [15] Gerken and Petersen (1992); [16] Heil *et al.* (1990); [17] Mills *et al.* (1985); [18] Silva *et al.* (2006); [19] Laursen *et al.* (2009); [20] Boelling *et al.* (2007); [21] Grindflek and Sehested (1996); [22] Stalder *et al.* (2004); [23] Quinton *et al.* (2011); [24] Boettcher *et al.* (1998); [25] Lundeheim (1987); [26] Fan *et al.* (2009); [27] Nkrumah *et al.* (2007); [28] Robinson and Oddy (2004); [29] von Felde *et al.* (1996); [30] Labroue *et al.* (1997); [31] Houston *et al.* (2005); [32] Howie *et al.* (2011); [33] Zhang *et al.* (2009); [34] Gilbert *et al.* (2009); [35] Craig *et al.* 1965 in Mignon-Grasteau and Faure (2002); [36] Wright *et al.* (2003); [37] Sartori and Mantovani (2010); [38] Riddel and Swain (1991); [39] Turner *et al.* (2009); [40] Vollestad and Quinn (2003); [41] Løvendahl *et al.* (2005); [42] Hellbrügge *et al.* (2008); [43] Kjaer and Sørensen (1997); [44] Su *et al.* (2005); [45] Craig and Muir (1993); [46] Buitenhuis *et al.* (2003); [47] Jonsson (1985); [48] Breuer *et al.* (2005); [49] Morris *et al.* (1994); [50] Le Neindre *et al.* (2002); [51] Hoppe *et al.* (2008); [52] Grandinson *et al.* (2003); [53] Vangen *et al.* (2005); [54] Grandinson *et al.* (2002); [55] Van der Steen *et al.* (1988); [56] Knap and Merks (1987); [57] Quilter *et al.* (2007); [58] Chen *et al.* (2009); [59] Xu *et al.* (2010); [60] Hemsworth *et al.* (1990); [61] Gauly *et al.* (2001); [62] Gill *et al.* (2007); [63] Hoppe *et al.* (2010); [64] Schmutz *et al.* (2001); [65] Holl *et al.* (2010); [66] Craig and Muir (1989); [67] Beaumont *et al.* (2005); [68] Minvielle *et al.* (2005); [69] Jones *et al.* (2009); [70] Schutz and Pajor (2001); [71] Visscher and Goddard (1995); [72] Hiendleder *et al.* (2003); [73] Burrow (2001).

Table 3 Genetic correlations (minimum/maximum) and identified chromosomal co-location between the behavioural response of animals to stressors in the physical and social environments and production traits in cattle, pig and poultry

Test	Stress applied	Behaviour trait	Cattle	Pig	Poultry
			D: Dairy; B: Beef		H: laying Hen; B: Broiler; T: Turkey
Response to the physical environment					
OPEN-FIELD ACTIVITY	ACUTE	LOCOMOTION	B: GROWTH* running time $-0.42/-0.37$ [1] B: GROWTH N attempts $-0.30/-0.24$ [1] B: MILK running time -0.25 [1] B: MILK N attempts -0.19 [1]		H: GROWTH activity QTL [21]
OPEN-FIELD ACTIVITY ON-FARM ACTIVITY	ACUTE CHRONIC	EXPLORATION LOCOMOTION	D: MILK lameness $0.24/0.48$ [2]	GROWTH leg action score $0.12/0.24$ [9] LEANNESS $-0.31/-0.24$ [9] FCR $-0.15/0.05$ [9] PROBORN $-0.11/-0.07$ [10] PROLOSS $-0.20/-0.05$ [10]	H: GROWTH novel object QTL [20] T: GROWTH walking $-0.37/-0.31$ [22] T: SURVIVAL walking $0.65/0.69$ [22]
ON-FARM ACTIVITY	CHRONIC	ACTIVITY			H: EGG ground pecking $-0.17/0.06$ [23] H: GROWTH contra-free-loading QTL [24] B: GROWTH $-0.08/0.07$ [25]
ON-FARM ACTIVITY	CHRONIC	DAILY FEEDING RATE	B: GROWTH 0.53 [3] B: LEANNESS $-0.22/-0.20$ [3] B: MEAT -0.39 [3] B: FCR -0.83 [3]	GROWTH $0.27/0.48$ [11, 12] LEANNESS $-0.25/-0.11$ [11, 12] MEAT $-0.30/-0.24$ [12] FCR $-0.21/0.03$ [11, 12]	B: FCR $-0.23/0.18$ [25] B: GROWTH $-0.15/-0.01$ [25]
ON-FARM ACTIVITY	CHRONIC	DAILY FEEDING FREQUENCY	B: GROWTH $-0.33/0.02$ [3, 4] B: LEANNESS $-0.13/-0.02$ [3, 4] B: MEAT $-0.73/-0.32$ [3, 4] B: FCR $-0.52/0.49$ [3, 4]	GROWTH $-0.19/0.04$ [11, 12] LEANNESS $0.10/0.15$ [11, 12] MEAT $0.15/0.23$ [11, 12] FCR $-0.19/0.11$ [11, 12]	B: FCR $-0.15/-0.01$ [25]
ON-FARM ACTIVITY	CHRONIC	DAILY FEEDING DURATION	B: GROWTH $-0.30/0.31$ [3, 4] B: LEANNESS $-0.38/0$ [3, 4] B: MEAT $-0.62/0.30$ [3, 4] B: FCR $-0.25/0.78$ [3, 4]	GROWTH $0.02/0.32$ [11, 12] LEANNESS $-0.15/-0.07$ [11, 12] MEAT $-0.11/0.08$ [12] FCR $0.12/0.16$ [11, 12]	B: FCR $-0.02/-0.01$ [25] B: GROWTH $-0.13/0.11$ [25] B: FCR $0.10/0.25$ [25]
Response to the social environment					
Relation to other group members					
SOCIAL MOTIVATION DYADIC ENCOUNTERS	ACUTE ACUTE	LOCOMOTION DOMINANCE		GROWTH 0.13 [13] LEANNESS -0.08 [13] MEAT -0.21 [13] PROBORN 0.15 [14]	H: GROWTH 1 QTL [24]
ON-FARM AGGRESSION [GROUP]	ACUTE	AGGRESSION			H: GROWTH delivery $0/0.66$ [26, 27] H: GROWTH gentle receipt QTL [21] H: EGG gentle delivery $-0.11/0.47$ [23] H: EGG severe delivery $-0.38/-0.11$ [23]
ON-FARM AGGRESSION [GROUP]	CHRONIC	AGGRESSION		GROWTH tail-biting 0.27 [15] GROWTH social rank -0.66 [16] LEANNESS tail-biting 0.28 [15] MEAT social rank 0.40 [16]	
Response of dam to progeny					
PROGENY REMOVAL	ACUTE	REACTIVITY	B: MILK 0.15 [1] B: PROGROWTH $-0.08/0.05$ [5]	TNB $-0.73/-0.26$ [14] PROGROWTH $-0.49/-0.13$ [17]	

Table 3 Continued

Test	Stress applied	Behaviour trait	Cattle	Pig	Poultry
			D: Dairy; B: Beef		H: laying Hen; B: Broiler; T: Turkey
Response to human or predator HANDLING SEPARATION	ACUTE	DOCILITY	B: GROWTH score $-0.22/0.07$ [1, 6] B: MILK index -0.20 score 0.07 [1] B: MILK running T -0.25 [1] B: MILK N escape -0.15 [1]		
HIGH RESTRAINT	ACUTE	MOTION	B: GROWTH score $-0.58/-0.13$ [7]	GROWTH score -0.38 [18] LEANNESS score $0.11/0.16$ [18]	
HIGH RESTRAINT	ACUTE	ESCAPE		GROWTH N struggle 0.38 [13] LEANNESS time struggle -0.14 [13] LEANNESS N struggle 0.08 [13] MEAT -0.03 [13]	
HIGH RESTRAINT	ACUTE	FLYING	B: GROWTH speed score $-0.41/-0.04$ [7] B: GROWTH speed -0.25 [4] B: LEANNESS speed: -0.36 [4] B: MEAT speed 0.81 [4] B: FCR speed 0.40 [4]	GROWTH time 0.14 [19] LEANNESS time -0.21 [19]	H: GROWTH immobility QTL [20]
ON-FARM OBSERVATION	ACUTE	MILKING	D: MILK speed $-0.34/0.06$ [8]		

QTL = quantitative trait loci; ECG = electrocardiogram; FCR = feed conversion ratio.

*GROWTH: growth rate; MILK: milk yield; LEANNESS: modified from results on backfat depth; MEAT: meat production assessed from muscle areas and carcass lean content; FCR: feed conversion ratio; TNB: total number born; PROGROWTH: progeny growth; PROBORN: progeny number born; PROLOSS: progeny loss. Precisions on the definition of the trait are specified where necessary.

[1] Phocas *et al.* (2006); [2] Lyons *et al.* (1991); Groen *et al.* (1995); Pryce *et al.* (1997); van Dorp *et al.* (1998) in Ingvarsten *et al.* (2003); [3] Robinson and Oddy (2004); [4] Nkrumah *et al.* (2007); [5] Hoppe *et al.* (2008); [6] Gauly *et al.* (2001); [7] Hoppe *et al.* (2010); [8] Visscher and Goddard (1995); [9] Serenius *et al.* (2001); [10] Serenius *et al.* (2004); [11] von Felde *et al.* (1996); [12] Labroue *et al.* (1997); [13] Velie *et al.* (2009); [14] Hellbrügge *et al.* (2008); [15] Breuer *et al.* (2005); [16] Jonsson (1985); [17] Grandinson *et al.* (2002); [18] Holl *et al.* (2010); [19] Jones *et al.* (2009); [20] Schütz *et al.* (2004); [21] Van der poel *et al.* in Buitenhuis *et al.* (2005); [22] Quinton *et al.* (2011); [23] Buitenhuis *et al.* (2004); [24] Schütz *et al.* (2002); [25] Howie *et al.* (2011); [26] Bessei (1984); [27] Su *et al.* (2005).

level, ease of locomotion is correlated positively with growth in pigs and milk yield in dairy cattle, whereas a negative correlation with growth was found in broilers (Table 3). In pigs, several QTL related to chronic activity were detected mainly on SSC5 and SSC7 and SSC8 (Reiner *et al.*, 2009). The QTL for chronic locomotion detected on SSC8 may be similar to the one for exploration in open field.

Using a divergent selection for dustbathing activity in quail, Gerken *et al.* (1988) found a negative relationship with fear-related traits (i.e. latency to emerge from a box and response to a tonic immobility test), which was interpreted as a response to the anxiety associated with not performing this maintenance activity. Later, Olsson and Keeling (2005) suggested that the selection operates directly on the fear response because dustbathing is realized only when the bird is not at risk of predation. The pre-laying behaviour of laying hens (sitting activity) is among the rare stereotypes observed in livestock. Experimental selection for this trait showed that the reestablishment of normal behaviour (increased sitting activity) is possible (Mills *et al.*, 1985). However, Beaumont *et al.* (2010) did not find sufficient ethical grounds to select for this behaviour, especially now that hens are reared on the floor instead of in cages, which increases their general activity and energy expenditure.

Feeding activity. In recent years, the genetics of feeding activity (duration, rate and frequency of visits to the food source) has been studied increasingly because of its relationship to feed efficiency, and because measurement has been facilitated by the use of automatic devices. Genetic variation in feeding activity exists in the three terrestrial species reviewed and shows large breed variation (e.g. cattle: Nkrumah *et al.*, 2007; pig: Labroue *et al.*, 1997; poultry: Howie *et al.*, 2011). Feeding frequency and feeding rate are more heritable (min = 0.38; max = 0.58) than feeding duration (Table 2). The genetic correlations between feeding behaviour (duration) and daily feed intake are null to positive in mammals and negative in broilers. Animals that show a genetic predisposition to eat more are known to grow faster but they also store more body fat than others. Growth is correlated favourably with feeding rate in cattle and pigs. Feeding rate is correlated unfavourably with meat production, whereas feeding duration and leanness show negative or null genetic associations (Labroue *et al.*, 1997; Robinson and Oddy, 2004). Growth and leanness are not genetically correlated with feeding frequency in pigs, but a G/A substitution at the MC4R gene (SSC1), which encodes a melanocortin receptor, has a positive effect on fatness, growth and daily feed intake, probably mediated through the central control of appetite (Kim *et al.*, 2000). Zhang *et al.* (2009) identified a QTL for the number of visits of pigs to the feeder on SSC7 that did not co-locate with QTL for feed intake and conversion neither to the QTL for feeding frequency (Houston *et al.*, 2005), and a suggestive QTL on SSC9 that may co-locate with a growth QTL. In broilers, feeding activity is not genetically correlated with growth (Howie *et al.*, 2011), which suggests that no substantial change in this activity has been induced by selective breeding in that species.

Residual feed intake (RFI) is a measure of feed efficiency that accounts for the animal's energy requirements for production and maintenance. The RFI indirectly measures the quantity of buffer resource available for global activity, and a genetic association between the two traits has been found in the three terrestrial species (hens: Braastad and Katle, 1989; Luiting and Urff, 1991; cattle: Richardson *et al.*, 1999; Herd *et al.*, 2004; pigs: Sadler *et al.*, 2011): animals with lower RFI are less active. Chronic frustration associated with the reduced feeding activity of the animals may also appear. Negative phenotypic correlations have been estimated between RFI and the response to acute stress in poultry and cattle (Luiting and Urff, 1991; Richardson and Herd, 2004; Rauw, 2007). The reduction of RFI by selection should increase feed efficiency, with a low impact on growth, but at the expense of reduced feeding activity, owing to its positive correlation with feeding duration (pig: $r_g = 0.44$, von Felde *et al.*, 1996; beef cattle: $r_g = 0.35$, Robinson and Oddy, 2004). Montanholi *et al.* (2010) observed that high-RFI steers make more visits to the feeder during the night than more efficient steers. Altan *et al.* (2004) found that low-RFI quail were less fearful, whereas Minvielle *et al.* (2002) did not find any significant correlation between RFI and the results of the tonic immobility test. In laying hens selected for lower RFI, reduced sensitivity to stress is observed under natural conditions (Schütz *et al.* 2002), but these genotypes are selected in cages.

Perspectives in selective breeding that account for behavioural adaptation to changes in the physical environment

Reducing the sensitivity of animals to stress is a major issue in the successful expansion of production. The strategies used to produce animals that are able to overcome the perturbations in their physical environment and return to homeostasis are dependent on the type of stress the animals face. On the one hand, Mormède *et al.* (2011) suggest that animals that produce a strong physiological response to acute stress adapt better to the stressor. The parallel cannot be made for behavioural responses where a phase of inhibition of all behavioural patterns is followed by a phase of activity. Selection for a greater activity or a greater exploration in the open field could be a strategy used to increase the capacity of livestock to adapt to acute stressors. However, in beef cattle, the genetic correlations of behavioural responses in the open-field test to production traits contradict this assumption. Conversely, a high degree of heritability has been found for latency to move and locomotion in laying hens. Selection for reduced reactivity to stress could be foreseen in that species to decrease the distress caused by changes in the physical environment. This strategy is acceptable provided that an optimum value is targeted, that favourable genetic correlations with production traits are estimated and that farming conditions are improved at the same time to avoid placing animals under conditions of stress.

When faced with long-term stressors or repeated modifications in their environment, animals with a lower perception of stress should be preferred to avoid large

unfavourable effects on production (Forkman *et al.*, 2007). Animals displaying more exploration might also show a higher behavioural adaptation in both the short and the long term; this trait deserves further genetic investigation. Abnormal behaviours (e.g. pre-laying behaviour in hens, circular shoaling in Atlantic salmon) show substantial genetic variation and heritability but have not been selected against because these reactions do not necessarily indicate poor welfare (Dawkins, 2004) and they may help the animal to cope with its physical environment.

Within a line or a rearing group, animals can exhibit different feeding strategies but achieve the same feed intake (Tolkamp *et al.*, 1998 in Howie *et al.*, 2011). This behavioural flexibility could be used for selective breeding in specific environments, especially in broilers, in which feeding behaviour shows low genetic correlation with growth. This strategy based on feeding behaviour traits could be complementary to strategies based on feed consumption if it is confirmed such as in pigs that different chromosomal regions affect the two traits categories. Selection for lower RFI is a sensitive approach that should be addressed with caution because it might reduce the buffer capacity of the animal in its reaction to stress (Rauv, 2007), especially under hot conditions. For instance, laying hens with high RFI cope better with high temperatures (Bordas and Minvielle, 1997) but are more fearful of humans (Schütz *et al.*, 2002) and do not require social reinstatement as strongly as hens with low RFI (Väisänen *et al.*, 2005).

Traits related to global activity (drinking and locomotion) are important indicators of animal welfare and, although less heritable, they are easier to record and analyse than health traits. Accounting for ease of locomotion in selective breeding may be a useful strategy to limit the deterioration of welfare observed in dairy cattle and broilers, and also to prevent lameness in pigs, if it were recorded at a young age. The genetics of chronic activity should be analysed in high-production genotypes because their heat tolerance is reduced compared with that of less productive animals (Ravagnolo and Misztal, 2000; Kadzere *et al.*, 2002; N'Dri, 2006; Gaughan *et al.*, 2010). The QTL approach of Reiner *et al.* (2009), used to analyse drinking activity in pigs, suggests that this trait has a polygenic determinism, which would make its selection more difficult. Reduction of the weight allotted to various production traits in breeding programmes may be a solution to improve the capacity of animals to adapt to hot conditions (Bessei, 2006).

Future studies will need to demonstrate that both acute and chronic responses are complementary in the development of resilience to sudden modifications in the physical environment, and in the eventual development of tolerance when the modification lasts for a long time.

Genetics of the behavioural response to changes in the social environment

Estimates of the heritability of behavioural responses to acute and chronic changes in the social environment are presented in Table 2, with distinction between cases in which the animal is

expected to react to environmental changes that involve other group members, progeny or the farmer. The genetic correlations with production traits are given in Table 3.

Interactions with other group members

Behavioural response to acute stress. The comfort provided by the presence of other group members after a period of isolation is a welfare-related concept that has been used in the estimation of the genetic tendency towards social motivation in quail and fish models. The experimental approach used to assess re-grouping in fish (shoaling) is similar to the social-reinstatement test used in quail, and is interpreted as an anti-predator response. Associated traits show moderate heritability (min = 0.22; max = 0.66). QTL were detected in the two species and an association with a QTL for growth was found in hen (Schütz *et al.*, 2004; Wright *et al.*, 2006). A large study was designed by Mills and Faure (1991) to test the genetic impact of social skills on growth, survival and other behaviours in Japanese quail. More social birds (high line) had more affiliation with other group members (use of distress calls), benefited from facilitated access to feed among the flock, performed more non-aggressive pecking and were more easily captured than less social birds (low line). Social motivation persisted in adulthood but was correlated with greater aggression. In subsequent generations, birds from the high line became more sensitive to both acute social stressors (mixing with unfamiliar animals) and chronic social stressors (rearing in large groups), and thus developed a lower capacity for adaptation. They showed social attraction towards any other group member, whereas quail from the low line showed bonding with familiar animals (Schweitzer *et al.*, 2009). Formanek *et al.* (2008) showed that selection to be also efficient when applied on juvenile quails.

Conversely, social aggression used to establish dominance is assessed most often with the resident–intruder test, which was developed for mice and then generalized to livestock species. Heritability shows mainly low values in mammals (min = 0; max = 0.36) and high values in fish ($h^2 > 0.40$; Table 2). Growth is reduced genetically in pigs that are aggressive towards intruders (Velie *et al.*, 2009). Measurement of aggressiveness within a group is an alternative procedure that elicits a response to crowding. In fish and poultry, social competition is evaluated mainly by measurement of survival rate and growth, but tests of aggression also exist (Table 1). The outcome of aggression refers to complex genetic determinism that depends on morphological aspects of the opponents (body weight and fur or feather pigmentation) and is strongly sex related.

Lahti *et al.* (2001) found evidence of a genetic basis for aggressive behaviour in brown trout; they observed that sea-run populations were more aggressive than lake-run or non-migratory populations. Conversely, Reinhardt (2001) did not find such a difference in Masu salmon. Divergent selection for plasma cortisol responsiveness to an acute confinement stress in trout showed that fish from the high line were more mobile in the presence of an intruder (Øverli *et al.*, 2002)

than fish from the low line; this suggests a link between fear and an aggressive response.

Aggression shows higher heritability in pigs than in poultry and salmon ($h^2 = 0.25$), with the duration of fighting after mixing being more heritable ($h^2 = 0.43$) than the number of aggressive episodes and the score of skin lesions (Turner *et al.*, 2009). A candidate gene approach emphasized that the AVPR1B gene, which encodes a vasopressin receptor, and the NR3C1 gene, which encodes a glucocorticoid receptor, are involved in the causation of aggression (Muráni *et al.*, 2010). Age was shown to be an important source of variation in hens, and the heritability of feather pecking increases with age. Buitenhuis *et al.* (2003) found different QTL on several chromosomes that were related to receiving feather pecking at young and adult ages. When attacker and receiver were distinguished, the heritability of being aggressive was moderate ($h^2 > 0.20$) and higher than that of receiving aggression in both pigs and poultry. Genetic correlations between aggression and growth vary among studies in poultry and pigs; they are unfavourable to production in salmon (Vollestad and Quinn, 2003). In hatcheries, strong genotype–environment interactions control aggression (Mesa, 1991; Vandeputte and Prunet, 2002). Selection for rapid growth yields a correlated response in aggression only when food is defensible (experiment on medaka: Ruzzante and Doyle, 1991). In Atlantic salmon, as in rainbow trout, the cortisol response to acute confinement (crowding) is highly heritable ($h^2 = 0.41$: Pottinger and Carrick, 1999; $h^2 = 0.50$: Fevolden *et al.*, 2002) and predicts the behavioural response of fish in a number of situations (Øverli *et al.*, 2006). With divergent selection, the highly responsive fish were more active but showed a slower return to feeding activity when placed in a novel environment than poorly responsive fish (Øverli *et al.*, 2005; Schjolden *et al.*, 2005). The social effects observed on growth relied on the mixing of lines with different personalities. Furthermore, Ruiz-Gomez *et al.* (2008) demonstrated the complexity of the relationship between line and behaviour; inconsistent changes in behaviour were shown after a change of country. Three suggestive QTL for cortisol response to confinement were mapped in sea bass (Massault *et al.*, 2010), and major genes for the same trait are suspected in rainbow trout (Vallejo *et al.*, 2009). Two studies of divergent selection for behavioural response in the resident–intruder test were implemented by Bakker (1985) and Francis (1984) on three-spined sticklebacks and paradise fish, respectively. The two experiments showed unequal responses but highlighted a common genetic basis of aggressiveness and sexual behaviour. The high line consisted almost entirely of males and the low line of females.

In the pig, aggression between sows is moderately heritable ($h^2 = 0.30$) and shows a low but favourable correlation with piglet production (Hellbrügge *et al.*, 2008). Assessments on rangeland show that the heritability of aggressiveness in cattle, although rarely estimated, is around 0.36 (Silva *et al.*, 2006).

Behavioural response to chronic stress. Social behaviour is associated positively with welfare in mammalian breeds that

are less intensively selected for production (Le Neindre, 1984; Breuer *et al.*, 2005). Social rank at the feeder is highly heritable in male pigs with genetic correlations unfavourable to growth but favourable to meat content in pigs (Jonsson, 1985). Behavioural responses to chronic stressors in the physical environment may translate into some stereotypes such as long-lasting deviant relationships with other group members and altered relationships with humans. For instance, in pigs, tail-biting is a redirected foraging behaviour that would correspond to the behaviour shown before feeding. Breuer *et al.* (2005) identified genetic variation in tail-biting in Landrace pigs ($h^2 = 0.27$) but none in Large White pigs. Wilson *et al.* (2010) performed a genome-wide association study in which different chromosomal regions were suggested to be associated with severe tail-biting. At the genetic level, tail-biting is correlated positively with growth and leanness (Breuer *et al.*, 2005).

It was shown recently that mild and severe feather pecking correspond to different neural mechanisms, which involve responses to acute and chronic stressors in hens (Hugues and Buitenhuis, 2010). Indeed, feather pecking is a normal behaviour, but when its intensity increases, it corresponds to a redirected behaviour (also related to foraging and exploration) that results from multiple causes, including fear (Keeling and Jensen, 1995). There is considerable breed variation in feather damage and cannibalism, and the phenotypic relationship between the two traits varies between populations. The heritability of feather pecking ranges from moderate to high values and severe pecking is correlated unfavourably to egg production (Buitenhuis *et al.*, 2004). The genetic analysis of feather pecking in hens is a topic on which much progress has been made in the last two decades towards a deep understanding of its biological pathways. There is evidence that many genes with minor effects are involved in the causation of feather pecking; QTL have been found, with a majority on GGA1. Keeling *et al.* (2004) showed that a QTL for feather damage in chickens coincided with the dominant white pigmentation locus. Biscarini *et al.* (2010) carried out a genome-wide association study and detected different chromosomal regions involved in feather damage in hens.

Laying hen populations divergently selected for feather pecking were created successfully in parallel to a control line (Kjaer *et al.*, 2001; Su *et al.*, 2005). More aggressive birds (high line) vocalized and walked for a longer time in an open-field test than birds from the low line (Jones *et al.*, 1995) in association with a neural hyperactive disorder. This was interpreted as indicating differences in social motivation. Flisikowski *et al.* (2009) demonstrated an association with a dopamine receptor, DRD4, on GGA5, which is known to be associated with exploration behaviour. The same kind of selection was implemented in naked-neck broilers by Boulay *et al.* (2006), who measured the number of pecks delivered on a bunch of feathers. Birds from the high line exhibited lower pecking activity and higher feather coverage. In fact, the animals reacted to the modification of their physical environment rather than the modification of their social environment. In both experiments, egg production was

lower in the high line. Feed efficiency was lower in hens from the high line as a result of their poor feather condition when compared with that of hens from the low line.

Female feather pecking is associated favourably with earlier egg-laying (Jensen *et al.*, 2005), but the egg production of those who show feather pecking is lower than that of non-peckers (Buitenhuis *et al.*, 2004).

Maternal behaviour

The survival of progeny depends strongly on maternal care during the first days of life. Bonding is more critical in cattle than in pigs because it is an exclusive link, which makes adoption more difficult in bovine species (Poindron, 2005). The intensity of stress is increased with human handling or with disruption of contact with the progeny. Several indications of maternal care after birth have been scored in cows (Grignard, 2001; Phocas *et al.*, 2006) and sows (Vangen *et al.*, 2005), in order to evaluate the behavioural response to acute and chronic social stressors (e.g. birth *v.* maternal ability during lactation). Higher heritability was observed for the reaction of the dam to removal of the newborn and handling by humans in beef cattle (~ 0.30) than in sows (Grandinson *et al.*, 2003; Hoppe *et al.*, 2008). Maternal ability score during lactation in pigs also shows low heritability (Vangen *et al.*, 2005). Heritability is higher in Herefords than in Angus cows and has been shown to vary with age in that breed (Hoppe *et al.*, 2008).

In pigs, abnormal maternal behaviour, including crushing but also savaging the progeny, is an important issue in female European lines. Savaging of progeny is moderately to highly heritable. On-farm assessment has been rarely analysed and provides very low values of heritability. The postural reaction of the female to a screaming piglet produced the highest estimate ($h^2 \sim 0.10$). This could be a sign of a higher genetic predisposition to react to involuntary crushing in some sows, and these sows also benefit from a higher genetic merit for progeny growth (Grandinson *et al.*, 2002). Several QTL related to maternal cannibalism have been observed, with a promising one on the X chromosome (Quilter *et al.*, 2007; Chen *et al.*, 2009). In hens, Xu *et al.* (2010) found three QTL involved in egg incubation behaviour, which was put at a disadvantage by selective breeding; among these QTL one was linked to the DRD1 gene, which encodes a dopamine receptor.

Phocas *et al.* (2006) found, in beef cattle, that the more maternal cows showed a slightly higher milking ability, but Hoppe *et al.* (2008) found no association of maternal reaction to progeny removal with progeny growth. Higher maternal ability is genetically correlated with lower progeny mortality in pigs (Grandinson *et al.*, 2003; Hellbrügge *et al.*, 2008), whereas Hoppe *et al.* (2008) found no genetic association in cattle.

Response to human or predator

Genetic influences on fear of humans have been identified by comparison of various genotypes and crosses in the four livestock productions (cattle, Morris *et al.*, 1994; poultry and

laying hens, Craig *et al.*, 1983; duck, Arnaud *et al.*, 2010; red jungle fowl, Håkansson *et al.*, 2007; rainbow trout, Woodward and Strange, 1987; pig, Terlouw, 2005). Fear of humans is correlated unfavourably with growth at the genetic level. Although the response to human handling is an important trait in fish, the heritability of associated behavioural traits has not been investigated, according to the literature. In zebrafish, the QTL detected for shoaling tendency could not be linked to QTL for growth or fatness (Wright *et al.*, 2006).

In cattle, there is large variation among breeds with respect to the fear of human handling. Limousine cows are more fearful than Jersey cows when reared in their natural environment, but the difference disappears if they are placed in a similar environment (Fisher *et al.*, 2001). Under moderate restraint, the heritability of the docility score is generally moderate, but it is higher in Simmental than in Limousine cows and null in Angus (Gauly *et al.*, 2001). Schmutz *et al.* (2001) found co-locating QTL involved in the determinism of a mobility score and habituation to handling with high restraint in beef cattle and suggested an association with genes encoding for dopamine receptors. The reaction of cattle to a crush or a weighing scale is assessed with a test that is used in the United States and Australia as an on-farm selection criterion for personality in calves (Fisher *et al.*, 2001; Beckman *et al.*, 2005), and this trait has the advantage of a null or negative association with growth. A few QTL that influence the unprovoked flight distance of cattle from a feeder, and habituation (represented by the difference in score between two repeats of the same behavioural test), have been detected and co-location or pleiotropic effects between them were found (Gutierrez-Gil *et al.*, 2008). Some QTL have been detected that are common to the test situations described above, on chromosomes BTA1, BTA5 and BTA9. In dairy cattle, behaviour at milking shows moderate heritability and a low but unfavourable genetic correlation with milk yield. A large favourable correlation between behaviour at milking and handling exists ($r_g = 0.74$), and neither trait is genetically correlated with aggression at feeding (Burrow, 1997). It would be of interest to investigate whether the QTL observed on BTA5 that are associated with ease of handling in dairy cattle and beef cattle refer to the same gene.

In pigs, the response to humans often implies a voluntary approach by the animal to the human, and shows higher heritability when assessed on animals isolated from other group members and when close contact with the human is assessed ($h^2 = 0.50$; Table 2). The flight score shows lower heritability in pigs than in cattle. A lower flight speed is correlated favourably with growth in both species, and with leanness in cattle but not in pigs. Vangen *et al.* (2005) found moderate heritability (min = 0; max = 0.22) for the response of sows to handling during routine management. The restraint-back test is commonly used in quail and pigs, although the subsequent tonic immobility induced by release of the animal is an innate anti-predator response in birds only (Gallup and Gordon, 1979). This test enables the assessment of emotional reactivity, which influences the facility of handling (Mignon-Grasteau and Faure, 2002) and relates to the coping strategies

of proactive and reactive animals. Restlessness during the back test shows an unfavourable genetic correlation with leanness in pigs (Velie *et al.*, 2009).

In poultry, the response of tonic immobility shows higher (moderate) heritability in pigs than in laying hens and Japanese quail (Table 2). Relationships to production traits are not obvious (e.g. Schütz *et al.*, 2004). In quail, Minvielle *et al.* (2002) observed the absence of genetic correlation between tonic immobility and production traits, which contradicts the hypothesis that fear and production are related. Similarly, the QTL found for the duration of tonic immobility did not co-locate with the QTL for growth and feed intake (Beaumont *et al.*, 2005; Minvielle *et al.*, 2005). In hens, different QTL influence fear of humans in birds of different ages and co-locate with QTL for exploration of a novel object. Divergent selection for the duration of tonic immobility was analysed extensively in Japanese quail by Mills and Faure (1991) and Jones *et al.* (1994) and in hens by Campo and Carnicer (1993). Quail selected for a long period of tonic immobility exhibit stronger fear reactions to various stimuli, human included (e.g. Minvielle *et al.*, 2002; Faure *et al.*, 2006).

Perspectives on selective breeding that account for behavioural adaptation to changes in the social environment

In fish, modifications observed in other livestock species, with respect to negative social interactions, should be considered to anticipate behavioural problems associated with intense selection for growth.

Selection against aggression, applied on young mammals, would be of double benefit if it also made dams more maternal (Løvendahl *et al.*, 2005; Hellbrügge *et al.*, 2008). Aggression and maternal behaviour are genetically correlated negatively in both the pig and some cattle breeds, making it possible to improve both behaviours. A strong limitation on their use in selection, however, is that social traits are poorly repeatable in these species (Janczak *et al.*, 2003; Hoppe *et al.*, 2008). However, selection against aggression and for ease of handling is promoted in beef cattle, and the use of a behavioural index is recommended (Gauly *et al.*, 2001; Benhajali *et al.*, 2010). In dairy cattle, Bowman *et al.* (1996) incorporated measurement of both docility and milking speed in their breeding programme, which had the objectives of reducing fear and increasing maternal care. There are also several sources of evidence of a positive genetic relationship between fear of humans and aggression in hens (e.g. Rodenburg *et al.*, 2004). In general, the behavioural response to humans can be related to social tendencies or maternal behaviour (in mammals) because fear modulates all reactions. Insights from research using fish models will help to increase the general understanding of the biological mechanisms behind fear and aggression. As in cattle, selection of pigs for docility can make sense, but the best genetic strategy to apply is not straightforward. The example of quail, which shows that selection for social motivation is successful at any age but that too great an increase in sociality is risky because it can increase aggression, ought to be kept in mind (Richard *et al.*, 2008). In any

species, optimum behaviour must be targeted in selective breeding in order to avoid deviant responses.

Although it is possible to select against behaviours genetically, the improvement of farm conditions is in many cases chosen as a solution to prevent stereotypes such as tail-biting activity in pigs. However, Craig and Adams (1984) considered that genetic selection is needed to reduce cannibalism in hens, together with feather pecking and injuries caused by escape and behaviour related to avoidance of humans. Feather condition might be useful as a criterion for selection, but discrepancies between studies are highlighted, which stresses the complexity of this social disorder and the attempt to develop realistic tactics. Beaumont *et al.* (2010) recommend selecting against mortality instead.

Attention should also be paid to the fact that, although the animal is the statistical unit used by geneticists, the group is often the unit studied by ethologists. Variation between and within breeds and populations in the behavioural response to stressors can be large. A major limitation to the success of selection for behaviour is the relationships with other group members, which make individual responses interdependent among the group. An indirect appreciation of sociality can be obtained with the use of social models for production traits. Bijma (2011) and Rutten *et al.* (2006) reported significant heritable components of social interactions that had effects on growth in beef cattle, laying hens, quail and pigs, but not in cod or Nile tilapia. This approach, which enables integration of both the animal's performance and its influence on that of other group members in the genetic evaluation, is attractive because it promotes sociality indirectly. Biscarini *et al.* (2010) showed the advantages of a social genetic model used to select against feather pecking in hens. A better understanding of the molecular mechanisms of action of the genes located on GGA1 (which have a strong effect on growth and a wide array of pleiotropic effects on welfare traits) may precede marker-assisted selection (Wirén and Jensen, 2010).

Conclusions

Accounting for behavioural traits in selective breeding could together improve animal welfare and improve production, reduce labour costs and increase handler safety. The four livestock productions studied do not face the same farming conditions and intensity of selection. The tests and behavioural traits used in experimental design are extrapolated from one species to another, but their validation as predictors of the animal's capacity to adapt to environmental changes is lacking. The rare genes identified that are associated with behaviour relate to motivational processes that demonstrate clearly that behavioural traits are important welfare indicators. Further genetic characterization, including the discovery of epistatic, pleiotropic and dominance effects among adaptive traits and production traits, and the use of high-output recording techniques are required for the development of strategies of selection. A synthetic variable that encompasses several traits recorded in different tests

may be more appropriate than a single-trait approach in selective breeding. Both behavioural and physiological measures should be implemented because they are interdependent in allowing the interpretation of the level of welfare (Dawkins, 2004).

Behavioural traits can be as heritable as some production traits that are considered for genetic improvement. The responses to both acute and chronic stressors need to be considered when analysing the capacity of an animal to adapt behaviourally to changes in the environment because they refer to different mechanisms of adaptation. In all species, some behavioural traits and production traits are controlled partially by the same pool of genes, either favourably in terms of improving both animal welfare and production (e.g. lower fear and growth) or unfavourably (e.g. feeding duration and feed efficiency in mammals). The results are influenced by the past history of selection of the species studied. Given the trade-off between fitness and production, it is time to define breeding goals that are more balanced between production and fitness traits (Kanis *et al.*, 2004; Olsson *et al.*, 2006; Barker, 2009). Knowledge of the genetics of behavioural adaptation will expand in the coming decades and should stimulate a greater dynamic in livestock breeding programmes.

References

- Altan O, Akbas Y and Aksit M 2004. Genetic variability of residual feed consumption (RFC) and its relationships with some production traits and fear response in Japanese quail hens (*Coturnix coturnix japonica*). *Archiv fur Geflugelkunde* 68, 223–229.
- Alvarez D and Nieceza AG 2003. Predator avoidance behaviour in wild and hatchery-reared brown trout: the role of experience and domestication. *Journal of Fish Biology* 63, 1565–1577.
- Arnaud I, Gardin E, Sauvage E, Bernadet MD, Couty M, Guy G and Guémené D 2010. Behavioral and adrenal responses to various stressors in mule ducks from different commercial genetic selection schemes and their respective parental genotypes. *Poultry Science* 89, 1097–1109.
- Bakker TCM 1985. Two-way selection of aggression in juvenile, female, and male sticklebacks (*Gasterosteus aculeatus* L.) with some notes on hormonal factors. *Behaviour* 93, 69–81.
- Barker JSF 2009. Defining fitness in natural and domesticated populations. In *Adaptation and fitness in animal populations: evolutionary and breeding perspectives on genetic resource management* (ed. J van der Werf, HU Graser, R Franckham and C Gondro), pp. 3–14. Springer, New York.
- Beaumont C, Lebihan-Duval E, Mignon-Grasteau S and Leterrier C 2010. The European experience in poultry welfare – a decade ahead. *Poultry Science* 89, 825–831.
- Beaumont C, Roussot O, Feve K, Vignoles F, Leroux S, Pitel F, Faure JM, Mills AD, Guémené D, Sellier N, Mignon-Grasteau S, Le Roy P and Vignal A 2005. A genome scan with AFLPTM markers to detect fearfulness-related QTLs in Japanese quail. *Animal Genetics* 36, 401–407.
- Beckman D, Speidel S, Brigham B, Garrick D and Enns R 2005. Genetic parameter estimates for docility in Limousin cattle. *Proceedings, Western Section, American Society of Animal Science* 56, 109–111.
- Beilharz RG, Luxford BG and Wilkinson JL 1993. Quantitative genetics and evolution: is our understanding of genetics sufficient to explain evolution? *Journal of Animal Breeding and Genetics* 110, 161–170.
- Benhajali H, Boivin X, Sapa J, Pellegrini P, Boulesteix P, Lajudie P and Phocas F 2010. Assessment of different on-farm measures of beef cattle temperament for use in genetic evaluation. *Journal of Animal Science* 88, 3529–3537.
- Bergeron R, Gonyou HW and Eurell TE 1996. Behavioral and physiological responses of Meishan, Yorkshire and crossbred gilts to conventional and turn-around gestation stall. *Canadian Journal of Animal Science* 76, 289–297.
- Bessei W 1984. Untersuchungen zur Heritabilität des Federpickverhaltens bei Junghennen. 1. Mitteilung. *Arch Geflügelk* 48, 224–231.
- Bessei W 1995. Genetics of feather pecking. *Proceedings of the 2nd European Poultry Breeders Roundtable, Foulum, 6–8 septembre 73*, 9–21.
- Bessei W 2006. Welfare of broilers: a review. *World's Poultry Science Journal* 62, 455–466.
- Bijma P 2011. Breeding for social interaction, for animal welfare. In *Encyclopedia of sustainability science and technology* (ed. RA Meyers). Springer Science and Business Media LLC, New York (in press).
- Biscarini F, Bovenhuis H, van der Poel JJ, Rodenburg TB, Jungerius AP and van Aendonk JAM 2010. Across-line SNP association study for direct and associative effects on feather damage in laying hens. *Behavior genetics* 40, 715–727.
- Bizeray D, Leterrier C, Constantin P and Faure JM 2000. Early locomotor behaviour in genetic stocks of chickens with different growth rates. *Applied Animal Behaviour Science* 68, 231–242.
- Boelling D, Fogh A and Nielsen US 2007. Locomotion as a new trait: first results from Denmark. *Interbull Bulletin* 37, 175–178.
- Boettcher PJ, Dekkers JC, Warnick LD and Wells SJ 1998. Genetic analysis of clinical lameness in dairy cattle. *Journal of Dairy Science* 81, 1148–1156.
- Boissy A, Le Neindre P, Gastinel PL and Bouix J 2002. Génétique et adaptation comportementale chez les ruminants: perspectives pour améliorer le bien-être en élevage. *INRA Productions Animales* 15, 373–382.
- Bordas A and Minvielle F 1997. Réponse à la chaleur de poules pondeuses issues de lignées sélectionnées pour une faible (R⁻) ou forte (R⁺) consommation alimentaire résiduelle. *Genetic Selection Evolution* 29, 279–290.
- Boulay M, Arnould C, Mignon-Grasteau S and Chapuis H 2006. Can plumage score be improved using an automatic measurement of pecking at a bunch of feathers? *Proceedings of the 8th World Congress on Genetics Applied to Livestock Production, Belo Horizonte, Brazil*, 174pp.
- Bowman PJ, Visscher PM and Goddard ME 1996. Customized selection indices for dairy bulls in Australia. *Animal Science* 62, 393–403.
- Branciarri R, Mugnai C, Mammoli R, Miraglia D, Ranucci D, Dal Bosco A and Castellini C 2009. Effect of genotype and rearing system on chicken behavior and muscle fiber characteristics. *Journal of Animal Science* 87, 4109–4117.
- Braastad BO and Katle J 1989. Behavioural differences between laying hen populations selected for high and low efficiency of food utilization. *British Poultry Science* 30, 533–544.
- Breuer K, Sutcliffe MEM, Mercer JT, Rance KA, O'Connell NE, Sneddon IA and Edwards SA 2005. Heritability of clinical tail-biting and its relation to performance traits. *Livestock Production Science* 93, 87–94.
- Buitenhuis AJ, Rodenburg TB, van Hierden YM, Siwek M, Cornelissen SJ, Nieuwland MG, Crooijmans RP, Groenen MA, Koene P and Korte SM 2003. Mapping quantitative trait loci affecting feather pecking behavior and stress response in laying hens. *Poultry Science* 82, 1215–1222.
- Buitenhuis AJ, Rodenburg TB, Siwek M, Cornelissen SJ, Nieuwland MG, Crooijmans RP, Groenen MA, Koene P, Bovenhuis H and van der Poel JJ 2004. Identification of QTLs involved in open-field behaviour in young and adult laying hens. *Behaviour Genetics* 34, 325–333.
- Buitenhuis AJ, Rodenburg TB, Siwek M, Cornelissen SJB, Nieuwland MGB, Crooijmans RPMA, Groenen MAM, Koene P, Bovenhuis H and van der Poel JJ 2005. Quantitative trait loci for behavioural traits in chickens. *Livestock Production Science* 93, 95–103.
- Burrow HM 1997. Measurements of temperament and their relationships with performance traits of beef cattle: a review. *Animal Breeding Abstracts* 65, 477–495.
- Burrow HM 2001. Variances and covariances between productive and adaptive traits and temperament in a composite breed of tropical beef cattle. *Livestock Production Science* 70, 213–233.
- Campo JL and Carnicer C 1993. Realized heritability of tonic immobility in White Leghorn hens: a replicated single generation test. *Poultry Science* 72, 2193–2199.
- Chen CF, Huang NZ, Gourichon D, Lee YP, Tixier-Boichard M and Bordas A 2008. Effect of introducing the naked neck gene in a line selected for low residual feed consumption, on performance in temperate or subtropical environments. *Poultry Science* 87, 1320–1327.
- Chen C, Guo Y, Yang G, Yang Z, Zhang Z, Yang B, Yan X, Perez-Enciso M, Ma J, Duan Y, Brenig B and Huang L 2009. A genome wide detection of quantitative trait loci on pig maternal infanticide behavior in a large scale White Duroc × Erhualian resource population. *Behavioural Genetics* 39, 213–219.

- Craig JV and Adams AW 1984. Behaviour and well-being of hens (*Callus domesticus*) in alternative housing environments. *World's Poultry Science Journal* 40, 221–240.
- Craig JV and Muir WM 1989. Fearful and associated responses of caged White Leghorn hens: genetic parameter estimates. *Poultry Science* 68, 1040–1046.
- Craig JV, Craig TP and Dayton AD 1983. Fearful behavior by caged hens of two genetic stocks. *Applied Animal Ethology* 10, 263–273.
- Craig JV, Jan ML, Polley CR and Bhagwat AL 1975. Changes in relative aggressiveness and social dominance associated with selection for early egg production in chickens. *Poultry Science* 54, 1647–1658.
- Craig JV and Muir WM 1993. Selection of reduction of beak-inflicted injuries among caged hens. *Poultry Science* 72, 411–420.
- Crump RE, Hansson AC, Graser HU and Sokolinski R 2005. Potential quantitative genetic indicators of pig temperament. Proceedings of the 16th Conference of the Association for the Advancement of Animal Breeding and Genetics, Noosa, Australia, pp. 91–94.
- Dado RG and Allen MS 1994. Variation in and relationships among feeding, chewing, and drinking variables for lactating dairy cows. *Journal of Dairy Science* 77, 132–144.
- Dantzer R 2001. Can farm animal welfare be understood without taking into account the issues of emotion and cognition? *Journal of Animal Science* 80 (E. suppl. 1), E1–E9.
- Dantzer R and Mormède P 1983. Stress in farm animals: a need for reevaluation. *Journal of Animal Science* 57, 6–18.
- Dawkins MS 2004. Using behaviour to assess animal welfare. *Animal Welfare* 13, S3–S7.
- Désautés C, Bidanel JP, Milan D, Iannuccelli N, Amigues Y, Bourgeois F, Caritez JC, Renard C, Chevalet C and Mormède P 2002. Genetic linkage mapping of quantitative trait loci for behavioral and neuroendocrine stress response traits in pigs. *Journal of Animal Science* 80, 2276–2285.
- Einum S and Fleming IA 1997. Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. *Journal of Fish Biology* 50, 634–651.
- Fabrega E, Font J, Carrión D, Velarde A, Ruiz-de-la-Torre J, Diestre A and Manteca X 2004. Differences in open field behaviour between heterozygous and homozygous negative gilts for the RYR(1) gene. *Journal of Applied Animal Welfare Science* 7, 83–93.
- Fan B, Onteru SK, Mote BE, Serenius T, Stalder KJ and Rothschild MF 2009. Large-scale association study for structural soundness and leg locomotion traits in the pig. *Genetics Selection Evolution* 41, 14.
- FAO (Food and Agriculture Organization) 2006. *Livestock's long shadow: environmental issues and options*, LEAD, FAO, Rome, 390pp.
- Faure JM, Arnould C, Beaumont C, Guemene D, Leterrier C, Mills AD and Richard S 2006. Consequences of selection for fear in Japanese quail. *Archiv für Geflügelkunde* 70, 216–222.
- Fevolden SE, Roed KH and Fjalestad KT 2002. Selection response of cortisol and lysozyme in rainbow trout and correlation to growth. *Aquaculture* 205, 61–75.
- Fisher AD, Morris CA, Matthews LR, Pitchford WS and Bottema CDK 2001. Handling and stress response traits in cattle: identification of putative genetic markers. In Proceedings of the 35th International Congress of the ISAE Center for Animal Welfare (ed. JP Garner, JA Mench and SP Heekin), pp. 100. UC Davis, Davis, CA, USA.
- Flisikowski K, Schwarzenbacher H, Wysocki M, Weigend S, Preisinger R, Kjaer JB and Fries R 2009. Variation in neighbouring genes of the dopaminergic and serotonergic systems affects feather pecking behaviour of laying hens. *Animal Genetics* 40, 192–199.
- Forkman B, Boissy A, Meunier-Salaun MC, Canali E and Jones RB 2007. A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. *Physiology and Behavior* 92, 340–374.
- Formanek L, Houdelier C, Lumineau S, Bertin A, Cabanès G and Richard-Yris MA 2008. Selection of social traits in juvenile Japanese quail affects adults' behaviour. *Applied Animal Behaviour Science* 112, 174–186.
- Frankham R 2009. Genetic architecture of reproductive fitness and its consequences. In *Adaptation and fitness in animal populations: evolutionary and breeding perspectives on genetic resource management* (ed. J van der Werf, HU Graser, R Frankham and C Gondro), pp. 15–40. Springer, New York.
- Francis RC 1984. The effects of bidirectional selection for social dominance on agonistic behavior and sex ratios in the paradise fish (*Macropodus opercularis*). *Behaviour* 90, 25–45.
- Gallup GG Jr and Gordon G 1979. Tonic immobility as a measure of fear in domestic fowl. *Animal Behaviour* 27, 316–317.
- Gaughan JB, Mader TL, Holt SM, Sullivan ML and Hahn GL 2010. Assessing the heat tolerance of 17 beef cattle genotypes. *International Journal of Biometeorology* 54, 617–627.
- Gauly M, Mathiak H, Kraus M and Erhardt G 2001. Estimating genetic variability in temperamental traits in German Angus and Simmental cattle. *Applied Animal Behaviour Science* 74, 109–119.
- Gentle MJ, Hughes BO, Fox A and Waddington D 1997. Behavioural and anatomical consequences of two beak trimming methods in 1- and 10-day old domestic chicks. *British Poultry Science* 38, 453–463.
- Gerken M and Petersen J 1992. Direct and correlated responses to bidirectional selection for dustbathing activity in Japanese quail (*Coturnix coturnix japonica*). *Behavioural Genetics* 22, 601–612.
- Gerken M, Bamberg H and Petersen J 1988. Studies of the relationship between fear related responses and production traits in Japanese quail (*Coturnix coturnix japonica*) bidirectionally selected for dustbathing activity. *Poultry Science* 67, 1363–1371.
- Gilbert H, Al Ain S, Bidanel JP, Lagant H, Billon Y, Guillouet P, Noblet J and Sellier P 2009. Divergent selection for residual feed intake in the growing pig: correlated effects on feeding behavior. Proceedings of the Research Swine Days, France, 41, 31–32.
- Gill CA, Boldt CR, Abbey CA, Wegenhoft MA, Lunt DK, Sawyer JE, Herring AD and Sanders JO 2007. Identification of QTL affecting disposition in *Bos indicus* influenced cattle. Proceedings of the Joint ADSA PSA AMPA ASAS Meeting Symposia, San Antonio, TX, Abstract no. 544.
- Gjerde B, Pante MJR and Baeverfjord G 2005. Genetic variation for a vertebral deformity in Atlantic salmon (*Salmo salar*). *Aquaculture* 244, 77–87.
- Grandin T and Deesing MJ 1998. Genetics and animal welfare. In *Genetics and the behaviour of Domestic Animals* (ed. T Grandin), pp. 113–144. Academic Press, San Diego, CA, USA.
- Grandinson K, Lund MS, Rydhmer L and Strandberg E 2002. Genetic parameters for the piglet mortality traits crushing, stillbirth and total mortality, and their relation to birth weight. *Acta Agriculturae Scandinavica Section A, Animal Science* 52, 167–173.
- Grandinson K, Rydhmer L, Strandberg E and Thodberg K 2003. Genetic analysis of on-farm tests of maternal behaviour in sows. *Livestock Production Science* 83, 141–151.
- Grignard L 2001. *Variabilité génétique des comportements sociaux chez les bovins domestiques (Bos taurus L)*. PhD thesis, Rennes I University, 147 pp.
- Grindflek E and Sehested E 1996. Conformation and longevity in Norwegian pigs. In Proceedings of the Nordiska Jordbruksforskarens Forening Seminar 265–Longevity of Sows. Research Centre Foulum, Denmark, pp. 77–83.
- Gutierrez-Gil B, Ball N, Burton D, Haskell M, Williams JL and Wiener P 2008. Identification of quantitative trait loci affecting cattle temperament. *Journal of Heredity* 99, 629–638.
- Håkansson J, Bratt C and Jensen P 2007. Behavioural differences between two captive populations of red jungle fowl (*Gallus gallus*) with different genetic background, raised under identical conditions. *Applied Animal Behaviour Science* 102, 24–38.
- Heil G, Simianer H and Dempfle L 1990. Genetic and phenotypic variation in pre-mating behavior of Leghorn hens kept in single cages. *Poultry Science* 69, 1231–1235.
- Hellbrügge B, Tölle KH, Bennewitz J, Henze C, Presuhn U and Krieter J 2008. Genetic aspects regarding piglet losses and the maternal behaviour of sows, Part 2. Genetic relationship between maternal behaviour in sows and piglet mortality. *Animal* 2, 1281–1288.
- Hemsworth PH, Barnett JL, Treacy D and Madgwick P 1990. The heritability of the trait fear of humans and the association between this trait and subsequent reproductive performance of gilts. *Applied Animal Behaviour Science* 25, 85–95.
- Herd RM, Oddy VH and Richardson EC 2004. Biological basis for variation in residual feed intake in beef cattle. 1. Review of potential mechanisms. *Australian Journal of Experimental Agriculture* 44, 423–430.
- Hiendleder S, Thomsen H, Reinsch N, Bennewitz J, Leyhe-Horn B, Looft C, Xu N, Medjugorac I, Russ I, Kühn C, Brockmann GA, Blümel J, Brenig B, Reinhardt F, Reents R, Averdunk G, Schwerin M, Förster M, Kalm E and Erhardt G 2003.

- Mapping of QTL for body conformation and behaviour in cattle. *Journal of Heredity* 94, 496–506.
- Holl JW, Rohrer GA and Brown-Brandl TM 2010. Estimates of genetic parameters among scale activity scores, growth, and fatness in pigs. *Journal of Animal Science* 88, 455–459.
- Hoppe S, Brandt HR, Erhardt G and Gauly M 2008. Maternal protective behaviour of German Angus and Simmental beef cattle after parturition and its relation to production traits. *Applied Animal Behaviour Science* 114, 297–306.
- Hoppe S, Brandt HR, König S, Erhardt G and Gauly M 2010. Temperament traits of beef calves measured under field conditions and their relationships to performance. *Journal of Animal Science* 88, 1982–1989.
- Houston RD, Haley CS, Archibald AL and Rance KA 2005. A QTL affecting daily feed intake maps to chromosome 2 in pigs. *Mammalian Genome* 16, 464–470.
- Howie JA, Avendano S, Tolkamp BJ and Kyriazakis I 2011. Genetic parameters of feeding behaviour traits and their relationship with live performance traits in modern broiler lines. *Poultry Science* 90, 1197–1205.
- Huff GR, Huff WE, Rath NC, Donoghue AM, Anthony NB and Nestor KE 2007. Differential effects of sex and genetics on behavior and stress response of turkeys. *Poultry Science* 86, 1294–1303.
- Hugues AL and Buitenhuis AJ 2010. Reduced variance of gene expression at numerous loci in a population of chickens selected for high feather pecking. *Poultry Science* 89, 1858–1869.
- Ingvartsen KL, Dewhurst RJ and Friggens NC 2003. On the relationship between lactational performance and health: is it yield or metabolic imbalance that causes diseases in dairy cattle? A position paper. *Livestock Production Science* 83, 277–308.
- Janczak AM, Pedersen LJ, Rydhmer L and Bakken M 2003. Relation between early fear- and anxiety-related behaviour and maternal ability in sows. *Applied Animal Behaviour Science* 82, 121–135.
- Jensen P, Keeling L, Schütz K, Andersson L, Mormede P, Brandstrom H, Forkman B, Kerje S, Fredriksson R, Ohlsson C, Larsson S, Mallmin H and Kindmark A 2005. Feather pecking in chickens is genetically related to behavioural and developmental traits. *Physiology and Behavior* 86, 52–60.
- Jones RB, Beuving G and Blokhuis HJ 1988. Tonic immobility and heterophil/lymphocyte responses of the domestic fowl to corticosterone infusion. *Physiology and Behavior* 42, 249–253.
- Jones RB, Blokhuis HJ and Beuving G 1995. Open-field and tonic immobility responses in domestic chicks of two genetic lines differing in their propensity to feather peck. *British Poultry Science* 36, 525–530.
- Jones RM, Hermesch S and Crump RE 2009. Evaluation of pig flight time, average daily gain and backfat using random effect models including growth group. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 18, 199–202.
- Jones RB, Mills AD, Faure JM and Williams JB 1994. Restraint, fear and distress in Japanese quail genetically selected for long or short tonic immobility reactions. *Physiology and Behavior* 56, 529–534.
- Jonsson P 1985. Gene action and maternal effects on social ranking and its relationship with production traits in pigs. *Journal of Animal Breeding and Genetics* 102, 208–220.
- Johnsson JI and Abrahams MV 1991. Interbreeding with domestic strain increases foraging under threat of predation in juvenile steelhead trout (*Oncorhynchus mykiss*): an experimental study. *Canadian Journal of Fisheries and Aquatic Sciences* 48, 243–247.
- Johnsson JI, Höjesjö J and Fleming IA 2001. Behavioural and heart rate responses to predation risk in wild and domesticated Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 58, 788–794.
- Kadzere CT, Murphy MR, Silznikove N and Maltz E 2002. Heat stress in lactating dairy cows: a review. *Livestock Production Science* 77, 59–91.
- Kanis E, van den Belt H, Groen AF, Schakel J and de Greef KH 2004. Breeding for improved welfare in pigs: a conceptual framework and its use in practice. *Animal Science* 78, 315–329.
- Keeling L and Jensen P 1995. Do feather pecking and cannibalistic hens have different personalities? *Applied Animal Behaviour Science* 44, 257–281.
- Keeling L, Andersson L, Schütz KE, Kerje S, Fredriksson R, Carlborg Ö, Cornwallis CK, Pizzari T and Jensen P 2004. Chicken genomics: feather-pecking and victim pigmentation. *Nature* 431, 645–646.
- Kim KS, Larsen N, Short T, Plastow G and Rothschild MF 2000. A missense variant of the porcine melanocortin-4 receptor (MC4R) gene is associated with fatness, growth, and feed intake traits. *Mammalian Genome* 11, 131–135.
- Kjaer JB and Mench JA 2003. Behaviour problems associated with selection for increased production. In *Poultry Genetics, Breeding and Technology* (ed. WM Muir and SE Aggrey), pp. 67–82. CAB International, Wallingford, UK.
- Kjaer JB and Sørensen P 1997. Feather pecking behaviour in White Leghorns, a genetic study. *British Poultry Science* 38, 333–341.
- Kjaer JB, Sørensen P and Su G 2001. Divergent selection on feather pecking behavior in laying hens (*Gallus gallus domesticus*). *Applied Animal Behaviour Science* 71, 229–239.
- Knap PW 2005. Breeding robust pigs. *Australian Journal of Experimental Agriculture* 45, 763–773.
- Knap PW and Merks JWM 1987. A note on the genetics of aggressiveness of primiparous sows towards their piglets. *Livestock Production Science* 17, 161–167.
- Koolhaas JM, de Boer SF and Bohus B 1997. Motivational systems or motivational states: behavioural and physiological evidence. *Applied Animal Behaviour Science* 53, 131–143.
- Labroue F, Guéblez R and Sellier P 1997. Genetic parameters of feeding behavior and performance traits in group-housed Large White and French Landrace growing pigs. *Genetic Selection and Evolution* 29, 451–468.
- Lahti K, Laurila A, Enberg K and Piironen J 2001. Variation in aggressive behaviour and growth rate between populations and migratory forms in the brown trout, *Salmo trutta*. *Animal Behaviour* 62, 935–944.
- Laursen MV, Boelling D and Mark T 2009. Genetic parameters for claw and leg health, foot and leg conformation and locomotion in Danish Holsteins. *Journal of Dairy Science* 92, 1770–1777.
- Le Bihan Duval E, Beaumont C and Colleau JJ 1996. Genetic parameters of the twisted legs syndrome in broiler chickens. *Genetics Selection Evolution* 28, 177–195.
- Le Neindre P 1984. La relation mère-jeune chez les ovins: influence de l'environnement social et de la race. Thèse de doctorat, Université de Rennes.
- Le Neindre P, Grignard L, Trillat G, Boissy A, Menissier F, Sapa J and Boivin X 2002. Docile Limousin cows are not poor mothers. *Proceedings of the 7th world congress on genetics applied to livestock production*, 19–23 August, 2002, Montpellier, comm. 14–13.
- Lepage O, Øverli Ø, Petersson E, Jarvi T and Winberg S 2000. Differential stress coping in wild and domesticated sea trout. *Brain Behaviour Evolution* 56, 259–268.
- Løvendahl P and Munksgaard L 2005. Are time-budgets of dairy cows affected by genetic improvement of milk yield? *Journal of Dairy Science* 88 (suppl. 1), 231.
- Løvendahl P, Damgaard LH, Nielsen BL, Thodberg K, Su G and Rydhmer L 2005. Aggressive behaviour of sows at mixing and maternal behaviour are heritable and genetically correlated traits. *Livestock Production Science* 93, 73–85.
- Luiting P and Uff EM 1991. Optimization of a model to estimate residual feed consumption in the laying hen. *Livestock Production Science* 27, 321–338.
- Lundeheim N 1987. Genetic analysis of osteochondrosis and leg weakness in the Swedish pig progeny testing scheme. *Acta agricultura Scandinavica* 37, 159–173.
- Mambrini M, Sanchez MP, Chevassus B, Labbé L, Quillet E and Boujard T 2004. Selection for growth increases feed intake and affects feeding behaviour of brown trout. *Livestock Production Science* 88, 85–98.
- Massault C, Hellems B, Louro B, Batargias C, Van Houdt KJ, Canario A, Volckaert FAM, Bovenhuis H, Haley C and de Koning DJ 2010. QTL for body weight, morphometric traits and stress response in European sea bass *Dicentrarchus labrax*. *Animal Genetics* 41, 337–345.
- McGlone JJ, Akins CK and Green RD 1991. Genetic variation of sitting frequency and duration in pigs. *Applied Animal Behaviour Science* 30, 319–322.
- Mercat MJ and Mormède P 2002. Influences génétiques sur les processus d'adaptation et le comportement alimentaire chez le porc. *INRA Productions Animales* 15, 349–356.
- Mesa MG 1991. Variation in feeding, aggression, and position choice between hatchery and wild cut throat trout in an artificial stream. *Transactions of the American Fisheries Society* 120, 723–727.
- Mignon-Grasteau S and Faure JM 2002. Génétique et adaptation: le point des connaissances chez les volailles. *INRA Productions Animales* 15, 357–364.

- Mignon-Grasteau S, Roussot O, Delaby C, Faure JM, Mills A, Leterrier C, Guéméné D, Constantin P, Mills M, Lepape G and Beaumont C 2003. Factorial correspondence analysis of fear-related behaviour traits in Japanese quail. *Behavioural Processes* 61, 69–75.
- Mignon-Grasteau S, Boissy A, Bouix J, Faure JM, Fisher AD, Hinch GN, Jensen P, Le Neindre P, Mormède P, Prunet P, Vandeputte M and Beaumont C 2005. Genetics of adaptation and domestication in livestock. *Livestock Production Science* 93, 3–14.
- Mills AD, Wood-Gush DG and Hughes BO 1985. Genetic analysis of strain differences in pre-laying behaviour in battery cages. *British Poultry Science* 26, 187–197.
- Mills A and Faure JM 1991. Divergent selection for duration of tonic immobility and social reinstatement behavior in Japanese quail (*Coturnix coturnix japonica*) chicks. *Journal of Comparative Psychology* 105, 25–38.
- Minvielle F, Mills AD, Faure JM, Monvoisin JL and Gourichon D 2002. Fearfulness and performance related traits in selected lines of Japanese quail (*Coturnix japonica*). *Poultry Science* 81, 21–326.
- Minvielle F, Kayang BB, Inoue-Murayama M, Miwa M, Vignal A, Gourichon D, Neau A, Monvoisin JL and Ito S 2005. Microsatellite mapping of QTL affecting growth, feed consumption, egg production, tonic immobility and body temperature of Japanese quail. *BMC Genomics* 6, 87.
- Montanholi YR, Swanson KC, Palme R, Schenkel FS, McBride BW, Lu D and Miller SP 2010. Assessing feed efficiency in beef steers through feeding behaviour, infrared thermography and glucocorticoids. *Animal* 4, 692–701.
- Mormède P, Foury A, Terenina E and Knap PW 2011. Breeding for robustness: the role of cortisol. *Animal* 5, 651–657.
- Morris CA, Cullen NG, Kilgour R and Bremner KJ 1994. Some genetic-factors affecting temperament in *bos-taurus* cattle. *New Zealand Journal of Agricultural Research* 37, 167–175.
- Muráni E, Ponsuksili S, D'Eath RB, Turner SP, Kurt E, Evans G, Thölking L, Klont R, Foury A, Mormède P and Wimmers K 2010. Association of HPA axis-related genetic variation with stress reactivity and aggressive behavior in pigs. *BMC Genetics* 11, 74–85.
- N'Dri AL 2006. Etude des interactions entre génotype et environnement chez le poulet de chair et la poule pondeuse. Thèse de l'INAPG, 249pp.
- Nkrumah JD, Crews DH, Basarab JA, Price MA, Okine EK, Wang Z, Li C and Moore SS 2007. Genetic and phenotypic relationships of feeding behavior and temperament with performance, feed efficiency, ultrasound, and carcass merit of beef cattle. *Journal of Animal Science* 85, 2382–2390.
- Nestor KE, Anderson JW, Patterson RA and Velleman SG 2008. Genetics of growth and reproduction in the Turkey. 17. Changes in genetic parameters over forty generations of selection for increased sixteen-week body weight. *Poultry Science* 87, 1971–1979.
- Olteneacu PA and Broom DM 2010. The impact of genetic selection for increased milk yield on the welfare of dairy cows. *Animal Welfare* 19, 39–49.
- Olsson IAS and Keeling LJ 2005. Why in earth? Dustbathing behavior in jungle and domestic fowl reviewed from a Tinbergian and animal welfare perspective. *Applied Animal Behaviour Science* 93, 259–282.
- Olsson IAS, Gamborg C and Sandøe P 2006. Thanking ethics into account in farm animal breeding: what can the breeding companies achieve? *Journal of Agricultural and Environmental Ethics* 19, 37–47.
- Øverli Ø, Winberg S and Pottinger T 2005. Behavioral and neuroendocrine correlates of selection for stress responsiveness in rainbow trout – a review. *Integrative and comparative biology* 45, 463–474.
- Øverli Ø, Pottinger TG, Carrick TR, Øverli E and Winberg S 2002. Differences in behaviour between rainbow trout selected for high- and low-stress responsiveness. *Journal of Experimental Biology* 205, 391–395.
- Øverli Ø, Sorensen C, Kiessling A, Pottinger TG and Gjoen HM 2006. Selection for improved stress tolerance in rainbow trout (*Oncorhynchus mykiss*) leads to reduced feed waste. *Aquaculture* 261, 776–781.
- Phocas F, Boivin X, Sapa J, Trillat G and Le Neindre P 2006. Genetic correlations between docility and other breeding traits in Limousin heifers. *Animal Science* 82, 805–812.
- Poindron P 2005. Mechanisms of activation of maternal behavior in mammals. *Reproduction Nutrition Development* 45, 341–351.
- Pottinger TG and Carrick TR 1999. Modification of the plasma cortisol response to stress in rainbow trout by selective breeding. *General and Comparative Endocrinology* 116, 122–132.
- Quilter CR, Blott SC, Wilson AE, Bagga MR, Sargent CA, Oliver GL, Southwood OI, Gilbert CL, Mileham A and Affara NA 2007. Porcine maternal infanticide as a model for puerperal psychosis. *American Journal of Medical Genetics Part B Neuropsychiatric Genetics* 144B, 862–868.
- Quinton CD, Wood BJ and Miller SP 2011. Genetic analysis of survival and fitness in turkeys with multiple-trait animal models. *Poultry Science* 90, 2479–2486.
- Raw WM, Kanis E, Noordhuizen-Stassen EN and Grommers FJ 1998. Undesirable side effects of selection for high production efficiency in farm animals: a review. *Livestock Production Science* 56, 15–33.
- Raw WM 2007. Physiological consequences of selection for increased performance. *Proceedings of the Conference of the Association for the Advancement of Animal Breeding and Genetics, Armidale, NSW, Australia*, 17, 240–247.
- Ravagnolo O and Misztal I 2000. Genetic component of heat stress in dairy cattle, parameter estimation. *Journal of Dairy Science* 83, 2126–2130.
- Reiner G, Kohler F, Berge T, Fischer R, Hubner-Weitz K, Scholl J and Willems H 2009. Mapping of quantitative trait loci affecting behavior in swine. *Animal Genetics* 40, 366–376.
- Reinhardt UG 2001. Selection for surface feeding in farmed and sea-ranched Masu Salmon juveniles. *Transactions of the American Fisheries Society* 130, 155–158.
- Richard S, Arnould C, Guemene D, Leterrier C, Mignon-Grasteau S and Faure JM 2008. Emotional reactivity in the quail: an integrated approach to animal welfare. *INRA Productions Animales* 21, 71–77.
- Richardson EC, Kilgour RJ, Archer JA and Herd RM 1999. Pedometers measure differences in activity in bulls selected for high or low net feed efficiency. *Proceedings of the Australian Society for the Study of Animal Behaviour* 26, 16.
- Richardson EC and Herd RM 2004. Biological basis for variation in residual feed intake in beef cattle. 2. Synthesis of results following divergent selection. *Australian Journal of Experimental Agriculture* 44, 431–440.
- Riddel BE and Swain DP 1991. Competition between hatchery and wild coho salmon (*Oncorhynchus kisutch*): genetic variation for agonistic behaviour in newly-emerged wild fry. *Aquaculture* 98, 161–172.
- Robinson DL and Oddy VH 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behaviour of feedlot finished beef cattle. *Livestock Production Science* 90, 255–270.
- Rodenburg TB, Buitenhuis AJ, Ask B, Uitdehaag KA, Koene P, van der Poel JJ, van Arendonk J and Bovenhuis H 2004. Genetic and phenotypic correlations between feather pecking and open-field response in laying hens at two different ages. *Behavior Genetics* 34, 407–415.
- Ruiz-Gomez M de L, Huntingford FA, Øverli Ø, Thörnqvist PO and Höglund E 2011. Response to environmental change in rainbow trout selected for divergent stress coping styles. *Physiology and Behavior* 102, 317–322.
- Ruiz-Gomez M de L, Kittilsen S, Höglund E, Huntingford FA, Sørensen C, Pottinger TG, Bakken M, Winberg S, Korzan WJ and Øverli Ø 2008. Behavioral plasticity in rainbow trout (*Oncorhynchus mykiss*) with divergent coping styles: when doves become hawks. *Hormones and Behavior* 54, 534–538.
- Rutten MJM, Bovenhuis H, Komen J and Bijma P 2006. Mixed model methodology to infer whether aggression increases due to selection on growth in aquaculture species. *Proceedings of the 8th World Congress of Genetics Applied to Livestock Production, Belo Horizonte*.
- Ruzzante DE and Doyle RW 1991. Rapid behavioral-changes in medaka (*Oryzias latipes*) caused by selection for competitive and noncompetitive growth. *Evolution* 45, 1936–1946.
- Sadler LJ, Johnson AK, Lonergan SM, Nettleton D and Dekkers JCM 2011. The effect of selection for residual feed intake on general behavioral activity and the occurrence of lesions in Yorkshire gilts. *Journal of Animal Science* 89, 258–266.
- Sartori C and Mantovani R 2010. Genetics of fighting ability in cattle using data from the traditional battle contest of the Valdostana breed. *Journal of Animal Science* 88, 3206–3213.
- Satterlee DG, Jones RB and Ryder FH 1993. Short-latency stressor effects on tonic immobility fear reactions of Japanese quail selected for adrenocortical responsiveness to immobilization. *Poultry Science* 72, 1132–1136.
- Schweitzer C, Poindron P and Arnould C 2009. Social motivation affects the display of individual discrimination in young and adult Japanese quail (*Coturnix japonica*). *Developmental Psychobiology* 51, 311–321.
- Schweitzer C and Arnould C 2010. Emotional reactivity of Japanese quail chicks with high or low social motivation reared under unstable social conditions. *Applied Animal Behaviour Science* 125, 143–150.

- Schjolden J, Backstrom T, Pulman KGT, Pottinger TG and Winberg S 2005. Divergence in behavioural responses to stress in two strains of rainbow trout (*Oncorhynchus mykiss*) with contrasting stress responsiveness. *Hormones and Behaviour* 48, 537–544.
- Schmutz SM, Stookey JM, Winkelman-Sim DC, Waltz CS, Plante Y and Buchanan FC 2001. A QTL study of cattle behavioral traits in embryo transfer families. *Journal of Heredity* 92, 290–292.
- Schutz MM and Pajor EA 2001. Genetic control of dairy cattle behavior. *Journal of Dairy Science* 84, E31–E38.
- Schütz K, Kerje S, Carlborg O, Jacobsson L, Andersson L and Jensen P 2002. QTL analysis of a Red Junglefowl × White Leghorn intercross reveals trade-off in resource allocation between behavior and production traits. *Behavioural Genetics* 32, 423–433.
- Schütz KE, Kerje S, Jacobsson L, Forkman B, Carlborg O, 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. *Behavior Genetics* 34, 121–130.
- Serenius T, Sevón-Aimonen ML and Mäntysaari EA 2001. The genetics of leg weakness in Finnish Large White and Landrace populations. *Livestock Production Science* 69, 101–111.
- Serenius T, Sevón-Aimonen ML, Kause A, Mäntysaari EA and Mäki-Tanila A 2004. Genetic associations of prolificacy with performance, carcass, meat quality, and leg conformation traits in the Finnish Landrace and Large White pig populations. *Journal of Animal Science* 82, 2301–2306.
- Shea-Moore MM 1998. The effect of genotype on behavior in segregated early-weaned pigs tested in an open field. *Journal of Animal Science* 76 (suppl. 1), 100.
- Silva B, Gonzalo A and Cañón J 2006. Genetic parameters of aggressiveness, ferocity and mobility in the fighting bull breed. *Animal Research* 55, 65–70.
- Stalder KJ, Knauer M, Baas TJ, Rothschild MF and Mabry JW 2004. Sow longevity. *Pig News and Information* 25, 53N–74N.
- Su G, Kjaer JB and Sørensen P 2005. Variance components and selection response for feather-pecking behavior in laying hens. *Poultry Science* 84, 14–21.
- Sundstrom LF, Petersson E, Hojesjo J, Johnsson JI and Järvi T 2004. Hatchery selection promotes boldness in newly hatched brown trout (*Salmo trutta*): implications for dominance. *Behavioural Ecology* 15, 192–198.
- Ten Napel J, Bianchi FB and Bestman M 2006. Utilizing intrinsic robustness in agricultural production systems. *Transforum, Zoetermeer, The Netherlands*.
- Terlouw EMC 2005. Stress reactions at slaughter and meat quality in pigs: genetic background and prior experience. A brief review of recent findings. *Livestock Production Science* 94, 125–135.
- Thomson JS, Watts PC, Pottinger TG and Sneddon LU 2011. Physiological and genetic correlates of boldness: characterising the mechanisms of behavioural variation in rainbow trout, *Oncorhynchus mykiss*. *Hormones and Behavior* 59, 67–74.
- Turner SP, Roehe R, D'Eath RB, Ison SH, Farish M, Jack MC, Lundeheim N, Rydhmer L and Lawrence AB 2009. Genetic validation of post-mixing skin injuries in pigs as an indicator of aggressiveness and the relationship with injuries under more stable social conditions. *Journal of Animal Science* 87, 3076–3082.
- Väisänen J and Jensen P 2003. Social versus exploration and foraging motivation in young red junglefowl (*Gallus gallus*) and White Leghorn layers. *Applied Animal Behaviour Science* 84, 139–158.
- Väisänen J, Lindqvist C and Jensen P 2005. Co-segregation of behavior and production related traits in an F3 intercross between red Junglefowl and White Leghorn laying hens. *Livestock Production Science* 94, 149–158.
- Vallejo RL, Rexroad III CE, Silverstein JT, Janss LLG and Weber GM 2009. Evidence of major genes affecting stress response in rainbow trout using Bayesian methods of complex segregation analysis. *Journal of Animal Science* 87, 3490–3505.
- Vandeputte M and Prunet P 2002. Génétique et adaptation chez les poissons: domestication, résistance au stress et adaptation aux conditions de milieu. *INRA Productions Animales* 15, 365–371.
- Vangen O, Holm B, Valros A, Lund MS and Rydhmer L 2005. Genetic variation in sows' maternal behaviour, recorded under field conditions. *Livestock Production Science* 93, 63–71.
- Van der steen HAM, Schaeffer LR, de Jong H and de Groot PN 1988. Aggressive behaviour of sows at parturition. *Journal of Animal Science* 66, 271–279.
- Velie BD, Maltecca C and Cassady JP 2009. Genetic relationships among pig behavior, growth, backfat, and loin muscle area. *Journal of animal science* 87, 2767–2773.
- Visscher PM and Goddard ME 1995. Genetic-parameters for milk-yield, survival workability, and type traits for dairy-cattle. *Journal of Dairy Science* 78, 205–220.
- Vollestad LA and Quinn TP 2003. Trade-off between growth rate and aggression in juvenile coho salmon, *Oncorhynchus kisutch*. *Animal Behaviour* 66, 561–568.
- von Felde A, Roehe R, Looft H and Kalm E 1996. Genetic association between feed intake and feed intake behavior at different stages of growth of group-housed boars. *Livestock Production Science* 47, 11–22.
- Wilson K, Zanella R, Ventura C, Johansen HL, Framstad T, Janczak A, Zanella AJ and Nelbergs HL 2012. Identification of chromosomal location associated with tail biting and being a victim of tail-biting behaviour in the domestic pig (*SUS Scrofa domestica*). *Journal of Applied Genetics* 53, 449–456.
- Wirén A and Jensen P 2010. A growth QTL on chicken chromosome 1 affects emotionality and sociality. *Behavioural Genetics* 41, 303–311.
- Woodward CC and Strange RJ 1987. Physiological stress response in wild and hatchery-reared rainbow trout. *Transactions of the American Fisheries Society* 116, 574–579.
- Wright D, Nakamichi R, Krause J and Butlin RK 2006. QTL analysis of behavioural and morphological differentiation between wild and laboratory zebrafish (*Danio rerio*). *Behavior Genetics* 36, 271–284.
- Wright D, Rimmer L, Pritchard VL, Krause J and Butlin RK 2003. Inter and intra-population variation in shoaling and boldness in the zebrafish (*Danio rerio*). *Naturwiss* 90, 374–377.
- Xu HP, Shen X, Zhou M, Luo CL, Kang L, Liang Y, Zeng H, Nie QH, Zhang DX and Zhang XQ 2010. The dopamine D2 receptor gene polymorphisms associated with chicken broodiness. *Poultry Science* 89, 428–438.
- Zhang ZY, Ren J, Ren DR, Ma JW, Guo YM and Huang LS 2009. Mapping quantitative trait loci for feed consumption and feeding behaviors in a White Duroc × Chinese Erhualian resource population. *Journal of Animal Science* 87, 3458–3463.