Breeding for behavioural change in farm animals: Practical, economic and ethical considerations

RB D'Eath[1], J Conington[1], AB Lawrence[1], IAS Olsson[2,3], P Sandøe[3]

[1] Sustainable Livestock Systems, SAC, UK
[2] IBMC- Instituto de Biologia Molecular e Celular, Universidade do Porto, Portugal
[3] Danish Centre for Bioethics and Risk Assessment, University of Copenhagen, Denmark

rick.death@sac.ac.uk

Abstract

In farm animal breeding, behavioural traits are rarely included in selection programmes despite their potential to improve animal production and welfare. Breeding goals have been broadened beyond production traits in most farm animal species to include health and functional traits, and opportunities exists to increase the inclusion of behaviour in breeding indices.

On the technical level, breeding for behaviour presents some particular challenges compared to physical traits. It is much more difficult and time-consuming to directly measure behaviour in a consistent and reliable manner in order to evaluate the large numbers of animals necessary for a breeding programme. For this reason, the development and validation of proxy measures of key behavioural traits is often required. Despite these difficulties, behavioural traits have been introduced by some breeders. For example, ease of handling is now included in some beef cattle breeding programmes.

While breeding for behaviour is potentially beneficial, ethical concerns have been raised. Since animals are adapted to the environment rather than the other way around, there may be a loss of 'naturalness' and/or animal integrity. Some examples such as breeding for good maternal behaviour could enhance welfare, production and naturalness, although dilemmas emerge where improved welfare could result from breeding away from natural behaviour. Selection against certain behaviours may carry a risk of creating animals which are generally un-reactive ("zombies"), although such broad effects could be measured and controlled. Finally breeding against behavioural measures of welfare could inadvertently result in resilient animals ("stoics") that do not show behavioural signs of low welfare yet may still be suffering. To prevent this, other measures of the underlying problem should be used, although cases where this is not possible remain troubling.

Keywords

Animal Welfare, Economics, Ethics, Genetics, Proxy measures, Selection index

Introduction

Breeding to change behaviour in farm animals has a number of possible benefits including improving production and product quality, reducing labour costs and improving handler safety (Jones & Hocking 1999; Boissy et al 2005; Grandinson 2005; Turner & Lawrence 2007; Macfarlane et al 2009). Breeding for behaviour could also be used to improve animal welfare, since many welfare problems may result from a mismatch between the environment and animal's range of coping responses (Fraser et al 1997). Normally, animal welfare scientists try to identify ways to correct this mismatch by changing the environment, although changing the animal by some means such as through genetic selection (Muir & Craig 1998; Jones & Hocking 1999; Kanis et al 2004) is a logical alternative.

Animal behaviour has undergone alteration throughout the history of domestication, and at first this was not deliberate: only relatively docile members of a species could be captured and/or herded, unmanageable animals were eaten rather than kept for breeding (Price 1984; Mignon-Grasteau et al 2005). Over the centuries selection became more deliberate, and is now carried out according to scientific principles in most farm animals, primarily to 'improve' production traits. Initially, relatively few traits such as growth rate, egg or milk yield were selected, but breeding goals have been refined by the addition of further traits relating to efficiency (feed conversion efficiency), or product quality (lean meat %, carcass composition, protein content of milk). In recent years, 'functional' traits relating to health, biological functioning and longevity have come to be included alongside traditional production traits in breeding indices, typically with an economic weighting (Lawrence et al 2004).

In general there is growing interest in how breeding may affect animal welfare in a negative or positive way. The Standing committee of the European convention for the protection of animals kept for farming purposes which covers all major farmed species (e.g. T-AP 1995; T-AP 1999; T-AP 2005a; T-AP 2005b) includes in its recommendations an article on 'changes of genotype' which emphasises that breeding goals should include health and welfare. Behavioural traits typically have heritability of a similar magnitude to traits already included in breeding programmes, making it technically possible to include behaviour, which is indeed already happening in some breeding programmes.

In this paper we will discuss a number of potential practical, economic and ethical issues which affect the feasibility and desirability of genetic selection for behaviour. We begin by outlining the process of animal breeding, introducing and defining concepts such as heritability, genetic correlation and selection indices. We then introduce the evidence that behaviour can be changed by genetic selection, discuss which behavioural traits have been investigated at the genetic level in farm animals, and which of these have been implemented in practice. We then describe some practical and economic factors affecting implementation, and finally discuss some ethical considerations.

Modern livestock breeding

The scientifically-based breeding (quantitative genetics) used in most farm animal species combines several desirable characteristics into a 'breeding index' or 'selection index' of overall merit (Hazel 1943). The relative emphasis placed on each trait depends on the other traits in the breeding objective. The rate of genetic change in a trait is therefore determined by its heritability (defined below), its genetic correlation with other traits in the index (defined below), the amount of variation seen in the population under selection and the relative importance placed on the trait by the breeder (usually determined by an overall breeding goal which is economic in the first instance).

The heritability of a trait can be described as the proportion of total variation that is genetic (rather than environmental) in origin on a scale of 0 to 1, and is used to determine an upper limit for how much genetic progress can be expected during selection. Traits with a high heritability are usually more readily altered through selection. The genetic correlation between two traits is a measure of the extent to which the same genes are responsible for influencing both traits, on a scale of -1 to +1. Although it is easier to make genetic progress with positively correlated traits, using selection index methodology, it is possible to make progress with traits that are antagonistically (unfavourably) correlated as long as the correlation between them is not close to 1.

Research into the genetics of behaviour

Behaviour is much more affected than physical traits by environmental influences either at the time (e.g. presence of group-mates or humans) or in advance of behaviour (e.g. learning or developmental influences). Nevertheless, there is still considerable evidence for genetic influences on behaviour. This evidence comes from the existence of species and breed differences, and studies involving quantitative genetics, artificial selection and gene knock-out studies (reviewed by Reif & Lesch 2003; Mormède 2005; Van Oers et al 2005). The variety and extent of behavioural change that has been documented in laboratory animal genetic studies (e.g. Miczek et al 2001; Finn et al 2003) indicates the potential for similar genetic changes in behaviour in farm animals.

In farm animals, heritability has been estimated for a number of behavioural traits that are of interest (most affect some aspect of production or welfare; Table 1). In many cases, estimated heritabilities are of comparable magnitude to traits already included in breeding programmes (around 0.1 to 0.4 REF), suggesting that selection for behaviour would be possible in principle.

TABLE 1 ABOUT HERE

In addition to the individual behaviours outlined in Table 1, other authors have proposed breeding goals which would be expected to affect more general aspects of behaviour. Such approaches include breeding to reduce fearfulness (Jones & Hocking 1999; Boissy et al 2005), stress reactivity (Mormède 2005), adaptability (Mignon-Grasteau et al 2005) or robustness (Kanis et al 2004). Concerns have been raised about the risks of breeding for traits with such wide effects (Mignon-Grasteau et al 2005).

A ‘group selection’ approach has been proposed as an indirect means to reduce negative social behaviour between animals. The idea here is that conventional quantitative genetic approaches can be altered to include the effect that animals have on each others’ production (Bijma et al 2007a; 2007b; Rodenburg et al 2009). In this way, negative behaviours such as damaging behaviour (feather pecking, cannibalism, tail biting) or aggressive behaviour (causing stress and excluding others from feeding) which affect production variables (survival, growth, egg production) can be indirectly reduced.

For example, groups of laying hens were left with their beaks not trimmed and entire groups were selected on the basis of longevity and egg production, resulting in lines which did not require beak trimming (Muir & Craig 1998). Considerable mortality was involved in this method which therefore should give rise to ethical concerns. A similar methodology has been applied to pigs (Bergsma et al 2008; Canario et al 2008). The actual effect on behaviour of applying this methodology can be assumed but as yet has not been studied in much detail. It may be expected that the methodology will result in general changes affecting more than one behaviour (Canario et al 2008; Rodenburg et al 2009).

Genetic selection for farm animal behaviour

For mink genetic research into various aspects of behaviour (exploration, fear of humans, aggression, activity, stereotypy, pelt- and tail-biting; reviewed by Vinke et al 2002) has shown that selection for behaviour is feasible; and selection experiments producing low fear (Malmkvist & Hansen 2001) and low stereotypy (Svendsen et al 2007) have taken place in Denmark. In Danish mink production animals are now selected against fur chewing (Malmkvist & Hansen 2001) and in the Dutch production they are selected against stereotypy and tail biting (Vinke et al 2002). The Standing committee of the European convention for the protection of animals kept for farming purposes (T-AP 1999), now recommends that for fur animals: "Strongly fearful animals should not be included in the breeding stock."

Cattle may be dangerous to handle, and temperament in response to human handlers (docility) has been used a criterion for genetic selection by the Limousin breed societies in Ireland and Australia and is now being introduced in Britain (Irish Limousin Cattle Society 2009; Australian Limousin Breeders Society 2009; British Limousin Cattle Society 2009). The methods used vary, but in Ireland, a 1-10 scale (aggressive to docile) is used depending on the response to a standard behavioural test in which a handler attempts to move an animal to one corner of a pen and hold it there (Le Neindre et al 1995). In many countries, temperament is scored in dairy cattle and recorded for inclusion in breeding indices. In the UK farmers rate their impressions of a cow on a 1-9 scale based on responses to milking (nervous to quiet, Pryce et al 2000).

Maternal behaviour in sheep (measured by a scoring system based around the proximity to the lamb during tagging) has been shown to have a heritability of around 0.13 (Lambe et al 2001). Efforts to improve this and other aspects of lamb vigour and maternal behaviour around parturition are now being implemented in the UK sheep industry (Conington et al 2009; Macfarlane et al 2009).

Although not actually selecting for behaviour, the change in breeding goal from litter size at birth to litter size at day 5 in the Danish pig industry (Su et al 2007) is likely to have a positive effect on aspects of maternal and neonatal behaviour that contribute to piglet survival.

Practical issues affecting the implementation of selection for behaviour

Measuring behaviour on the thousands of animals necessary to implement a breeding programme raises a number of practical issues. The labour costs of measuring behaviour by observation are high even for R&D, but are often prohibitive for practical implementation. To reduce these costs, quick behavioural tests (e.g. 'stick' test in mink, Malmkvist & Hansen 2001), automated measurement (e.g. flight speed from a crush in Beef Cattle, Burrow 1997) or proxy traits (e.g. skin lesion number as a proxy for aggressive behaviour; Turner et al 2006a; 2009a; 2009b) could be used. The use of proxy traits as indicators of a more difficult-to-measure breeding goal trait is common practice in breeding programmes (e.g. white blood cell counts in milk as an indirect indicator of mastitis in dairy cows; Pryce et al 1998). Behavioural problems which occur in sudden unpredictable outbreaks (e.g. hysteria, cannibalism and feather pecking in poultry; tail, ear and flank biting in pigs) are particularly problematic to study. There is a need for validated proxy measures that can be applied to animals in a ‘baseline’ state which are predictive of their behaviour during an outbreak (e.g. Breuer et al 2001; Statham et al 2006).

There may however be unintended consequences of using proxy measures. For example, breeding for slow flight speed in cattle in the hope of selecting calm animals might result in animals which were slow for another reason (e.g. because they were lame), or that breeding for few skin lesions 24hrs after mixing to reduce aggression in pigs could result in blunt teeth rather than less fighting. To avoid these sorts of problems, the goal trait must be clearly defined, and the genetic correlation between the goal and proxy trait should be re-examined as breeding progresses.

Regardless of the recording method (behavioural observations, tests, scoring systems) inter-observer reliability could be more of an issue for behaviour in comparison to simple to measure traits such as weight or milk yield. This is especially a problem for multiple farm breeding programmes where there is a single (different) scorer on each farm with limited cross-checking (e.g. beef or sheep). In practice, even with these problems, behaviour traits are heritable albeit at a low level (e.g. Pryce et al 2000). Poorly designed scoring systems for behaviour, are likely to result in unexplained non-genetic sources of variability in a trait and hence low heritability making it unlikely that a trait will be adopted by breeders. Well designed, research-based objective scoring systems (Macfarlane et al 2009) or (validated) use of automation (e.g. image analysis for feather scoring or skin lesion scoring) provide potential solutions.

Potentially, the use of molecular markers or genome-wide selection could provide a cost-effective way of selecting for behaviour, once the initial (expensive) research to identify the genetic signature of a behaviour has been done (Désautés et al 2002; Mormède 2005; Quilter et al 2007; Gutierrez-Gil et al 2008). However, as with any proxy trait, there is an ongoing need to check the results against the actual behavioural phenotype for certain animals every 2-3 generations. The genes or genome regions affecting differences in behaviour are likely to vary with breed/country so there is a need for validation against phenotype in each case.

Regardless of the trait and the method of measurement, genetic progress will be more rapid if we better estimate the genetic component of variance; this is perhaps an especially important point for behavioural selection given the sensitivity of behaviour to short and long-term environmental influences. This requires environmental conditions to be standardised or at least recorded (Mormède 2005) so that they can be included in the statistical models used for genetic analysis.

Economic drivers and bottlenecks affecting the implementation of selection for behaviour

In most farmed species, breeding goals are primarily aimed at production traits and the relative weighting of traits in the selection index depends on their economic importance (Brascamp et al 1985; Dekkers & Gibson 1998). There are a number of examples where this has resulted in reduced welfare through unfavourable outcomes in health, welfare and fitness characteristics, (see reviews by Rauw et al 1998; Jones & Hocking 1999; Sandøe et al 1999). These traits were not recorded so the effects of breeding on them were unknown or ignored. To address these problems, breeding goals have been broadened in a number of species (e.g. sheep and dairy cows) to include more traits (Simm 1998; Lawrence et al 2004; Pryce et al 2004).

It is important to note that many behavioural traits have an economic value. Thus by analogy one reason to include health traits in Scandinavian dairy breeding is that for the farmer, costs associated with mastitis (veterinary treatment, rejected milk) may offset the gains from increased production (Christensen 1998). Although inclusion of behavioural traits in breeding indices may constitute an improvement on animal welfare relative to not including them, their inclusion at economically determined weights may only result in slowing or halting in the growth of a problem, in particular if heritability is low or there is unfavourable genetic correlation with other traits in the index (Nielsen et al 2006; Nielsen & Amer 2007).

Some behavioural traits such as neonate survival or maternal behaviour may be of sufficient economic weight to result in positive changes in animal welfare if implemented. For other behavioural traits though, the economic value might be more difficult to quantify, even though the outcomes might be desirable for farmers. For example, large animals which are calm rather than reactive during handling could have benefits for reduced labour costs, increased handler safety and meat quality (Turner & Lawrence 2007) which are difficult to quantify in economic terms.

Society might wish behavioural traits to be improved more rapidly or even desire the inclusion of some traits that enhance welfare at the expense of production (Olesen et al 2000; McInerney 2004). How could this be achieved? Methods to quantify the societal benefits of broader breeding programmes and to estimate the non-market value of various traits have been proposed (Olesen et al 2000; Nielsen et al 2006; Nielsen & Amer 2007). Nevertheless, some traits will not have any economic value for the individual farmer, and including them in the breeding goal may even come at an economic cost, as this slows down the progress for traits that directly affect producer-income. Implementation of breeding for such traits will only take place if special incentives are provided. Analogous problems arise for other kinds of traits related to public goods such as reduced environmental impact (Olesen et al 2000; Kanis et al 2005).

Rules to ensure animal welfare relating to animal transport, housing and slaughter conditions are set by legislators, assurance schemes and retailers. Currently despite the existence of recommendations on breeding by a number of bodies including FAWC (2004), AEBC (2002) and the EU's T-AP committee (e.g. T-AP 1995; T-AP 1999; T-AP 2005a; T-AP 2005b) there is, however, very little regulation of breeding goals (Lawrence et al 2004). Existing EU legislation in this area has so far been ineffective (Olsson et al 2006).

Decision making over breeding goals varies according to the species involved. In pigs and poultry, a few global breeding companies control breeding and determine the breeding goals (in response to customer needs). Dairy cattle breeding is much more diverse in terms of ownership of pedigree animals, although genetic evaluations are centralised. Estimated breeding values for each bull for each trait are published, allowing farmers (to some extent) to make decisions about which traits to focus on when purchasing semen.

In the UK sheep and beef industries, some farmers make use of schemes which enable breeding index methodology to be applied to systematically improve certain traits, but a substantial number of pedigree breeders do not. Thus, there is for these breeds some room not only for breeding organizations but also for individual farmers to consider additional traits other than production traits in breeding.

In the EU, there has been an initiative of self-regulation by breeders: the Code of Good Practice for European Farm Animal Breeding and Reproduction (CODE-EFABAR, Neeteson-van Nieuwenhoven et al 2006) and some voluntary engagement by individual breeding companies with ethicists (Olsson et al 2006).

Presently under schemes such as organic, Freedom Foods or Products of Protected Origin, consumers pay premium prices for products with perceived added value in terms of production system. However, as opposed to production systems, consumers are unlikely to be aware of the role of breeding, and it being such a small part of the production process will probably make it difficult to justify a price increase (Olsson et al 2006). This may however be different if existing labelling schemes would also incorporate breeding as part of their requirements. At present, this is only done indirectly, as when assurance programs require animals of a certain breed such as slow-growing broilers (Cooper & Wrathall 2009) or locally adapted animals.

Ethical issues arising from selection for behaviour

Many people feel that limits should be placed on our interference with nature (Banner 1995; AEBC 2002; Macnaghten 2004). And it should be expected that this feeling might be strong in cases where we are tangling with complex aspects of animals' natures such as the genetic basis for their behaviour. Along with an animal's feelings and state of health (Fraser et al 1997), the opportunity to express normal (or natural) behaviour is seen as an important aspect of animal welfare, and it is one of FAWC's five freedoms (FAWC 2004).

The call for ethical limits can be defended in two rather different ways. It can be claimed either that we should refrain from interfering because we cannot accurately foresee the consequences of what we are doing and may therefore bring about some kind of disaster, or alternatively that we should leave nature as it is because untouched nature has a value of its own (Banner 1995; AEBC 2002; Macnaghten 2004).

According to the first line of thought the problem with interfering is that we cannot properly predict the long-term consequences of what we are doing. If we try to manipulate nature on the basis of 'grand plans' for the future, there is a real danger that unexpected and harmful consequences occur – as indeed it has sometimes happened for example when species of animals have been introduced by humans in new territory.

According to the other line of thought the problem with interfering with nature is that we should respect what is seen as the *integrity* of nature. It is seen as perverse and wrong that we try to shape animals according to our plans rather than leaving them to be the kind of creatures they are. Of course, in the context of farm animal breeding it may sound a bit weird to appeal to the idea that it is wrong to change animals to fit our goals – since that in a way is the *raison d'etre* of animal breeding. However, some argue that integrity comes in degrees and that it is a bigger concern to manipulate the behaviour of a dairy cow than it is to manipulate its disease resistance or length of calving intervals (Siipi 2008).

Changing the holes or the pegs?

Animal welfare problems often result where there is a mismatch between an animal's coping ability and the range of challenges offered by the environment (Fraser et al 1997). Bernard Rollin (2002) has characterised intensively farmed animals as square pegs forced into round holes; and breeding to make the animals fit the environment may be seen as an attempt to change the pegs rather than the holes.

Changing the environment to suit the animal is usually seen as the solution, but why is this ethically preferable to changing the animal to suit the environment? Concerns over animal naturalness or integrity are the issue here. In addition, since biology appears to impose few limitations on what is possible, changing the animal to suit the environment raises the question of the ethical acceptability of the environment. In a discussion of how breeding could be used to improve pig welfare, Kanis et al (2004) recognised that breeding animals adapted to tolerate poor environments might result in a decline in housing or husbandry practices.

To address this problem, Lawrence et al (2001) proposed that we should begin by defining 'Ethical Environment Envelopes' and then breed animals to have good welfare within these. There are a number of examples where breeding for behaviour could suit animals to more extensive housing systems which may be viewed as ethically more desirable than the alternative intensive housing systems. For example, selection for good maternal and neonatal behaviour in pigs could facilitate a move away from confinement housing, and selection to reduce feather pecking in barn and free-range laying hens will make the move away from cages easier and might reduce the need for beak trimming. Similarly, extensive systems for sheep could be made easier by breeding for animals that are disease resistant and do not require shearing, tail docking or close supervision at lambing (Conington et al 2009).

In intensive systems, even though it is more controversial, an argument could be made for pragmatism and accepting genetic selection for behaviour as part of the solution for welfare problems. For example, tail-biting in pigs could be reduced by the provision of more space and particularly improved access to substrates for rooting and chewing. However, the vast majority of pig farms in the EU do not provide adequate substrates and painful tail docking is widely applied. Tail docking removes the welfare problem for the bitten pig, but not for the biter- it simply masks the fact that these pigs still lack a suitable outlet for their motivation to root and chew on something.

Selection to reduce tail biting is ethically less attractive than providing suitable substrates, since it compromises the pig's integrity, particularly if accompanied by a correlated reduction in other behaviours which could be seen as being central to 'pigness' such as rooting and chewing. On the other hand if the alternative is tail docking breeding to reduce tail biting may be seen as the smaller of two evils. Thus a balance needs to be struck. If we accept that pigs are going to continue to be kept in systems without suitable substrates, then should we select against tail biting to improve pig welfare and removing the need for tail docking at the risk of compromising the pigs' integrity?

To take a different example, are we content with the 'unnatural wolf' (the dog) which is happier in a domestic setting because it has no desire to hunt? Isn't this better than a 'natural' wolf-like dog which is prevented from hunting? Of course, it may be argued that much effort is put into ensuring that dogs live reasonable lives; whereas breeding against tail biting in pigs could be seen as a too easy solution to the problem.

Zombies

One specific scenario, of particular concern to those concerned with animal integrity, is that animals may become extremely inactive or generally un-reactive to external stimuli as a result of breeding for behaviour. To simplify matters let us call these animals "zombies".

Reduced responsiveness to humans in particular (docility) and to environmental stimuli in general has been a major feature of behavioural change throughout domestication (Price 1984), so further change in this direction could be thought of as purely a continuation of the domestication process (Jones & Hocking 1999). Some authors have proposed selection for animals that are less reactive to stress or less fearful across a wide range of situations (Jones & Hocking 1999; Mignon-Grasteau et al 2005), and the 'zombie' criticism would apply to this kind of breeding. Indeed, Mignon-Grasteau et al. (2005) acknowledge the need for an ethical debate in wider society before such proposals could be taken forward. Even when a single trait is the focus of selection, genetic correlations between traits mean that the impact could be wider: Pigs which were genetically less aggressive at mixing were also less reactive at weighing (D'Eath et al 2009; Turner et al 2009a).

The issue of Zombies is clearly a problem for those advocating animal integrity. But why should it matter from the point of view of an animal that it has a smaller number of preferences and desires – as long as the desires that the animal does have are being satisfied? After all isn't animal welfare all about making sure that there is a fit between what an animal needs or prefers and what it gets? (Sandøe 1996)

To answer this question one may seek inspiration from the utilitarian philosopher John Stuart Mill (1863) who argued that "*It is better to be a human being dissatisfied than a pig satisfied; better to be Socrates dissatisfied than a fool satisfied. And if the fool, or the pig, are a different opinion, it is because they only know their own side of the question."* The idea would be that breeding zombie animals is problematic because it means reducing the value of the animal lives that comes out of the process.

The thought experiment of deliberately breeding animals with reduced sentience (a reduced capacity for higher mental states) was considered in the Banner report (Banner 1995) as being 'objectionable in its own right'. Others have expressed concern that reduced sentience could inadvertently result from selection for behavioural change (Paragraph 110, FAWC 2004).

Of course, since animal sentience is difficult to prove or measure it is difficult to address these issues in practice. However even in theory they may be a disagreement between those who think that animal welfare is all about making sure that animals get what they need and want and those who think that a higher level of needs and wants makes room for a richer and better life. The authors of this paper tend to side with the former.

Stoics

A very different scenario from the one just discussed is that animals are being bred to change behaviour, but they still experience the negative feelings associated with the unwanted behaviour. These animals we shall here call stoics, because outward signs of suffering appear to be reduced. This scenario could perhaps be thought of as falling within the ethical concern of 'unintended consequences'.

In relation to disease or parasitism, the concepts of resistance and resilience have subtly different meanings. Resistant animals do not become infected at all, while resilient animals are able to function better (growing and reproducing) despite being infected (Albers et al 1987). If one were to infect a population and just measure growth rate, these two classes of animals might appear similar, while from a welfare perspective resistance is surely preferable to resilience.

An analogous situation could occur when breeding to change behaviour, where stoics could be thought of as similar to resilient animals. Genetic selection directly on a trait which is used to measure welfare might mean that the trait becomes a less reliable indicator of welfare: A thought experiment here might be, that selection to improve locomotion score in lame animals could result in animals which still have the underlying problem (with bad feet or joint problems) but which do not show it. Selection to change behaviour without understanding the mechanism of that change could result in the mental equivalent of lameness (e.g. high fearfulness could result in inactivity).

Whenever possible, direct examination of the source of the problem is important to prevent such undesired effect (e.g. Conington et al 2009). However, as illustrated by the discussion around the example provided by Mills and co-workers (Mills et al 1985a; 1985b), this may not be straightforward. These researchers reduced stereotypic pacing behaviour in poultry by selecting against the amount of pre-laying pacing. Mason et al (2007) argued that this would be more likely to result in an improvement in welfare than selection against the stereotypy itself, because pre-laying pacing was an indicator of motivation to find a nest, so the root cause of the stereotypy had been altered. However, Appleby and Hughes (1991) argued that it had not been established whether reduced pre-laying pacing indicated that these animals actually experienced less frustration in the absence of a nest.

Muir and Craig (1998) describe another example: “Duncan and Filshie (1980) showed that a flighty strain of birds that exhibited avoidance and panic behaviour following stimulation returned to a normal heart beat sooner than a line of more docile birds, implying that the docile birds may be too frightened to move”. Different species of penguins (in the wild) differ in their behavioural reactivity to approaching humans

(Holmes 2007), but even penguins who show little behavioural reaction may show prolonged elevations in heart rate, suggesting that they experience an emotional response (Nimon et al 1995; Ellenberg et al 2006). Thus the link between emotional state and outward behaviour is not straightforward and must be understood before beginning on a selection programme to change behaviour.

When a welfare end-point, such as the level of stereotypic behaviour is directly selected against (e.g. by the mink industry in the Netherlands; Vinke et al 2002), this could present an example of selecting only against the symptoms while masking an underlying problem (Mason et al 2007). Indeed high stereotyping mink often have lower endocrine stress responses than low stereotyping mink, suggesting that it is a successful coping mechanism (Mason & Latham 2004). Svendsen et al (2007) found that low stereotypy was associated with high levels of fear of humans.

Kanis et al (2004) propose that experiments in which animals learn a task to express their environmental preferences could be used in selection. “It could be a practical option to breed for pigs which are less motivated to improve or change their situation and are thus sufficiently satisfied”. There is a risk that this approach might result in stoical pigs which do not act to remove themselves from stress, apathetic inactive pigs, or even those which are poor at learning such tasks.

There is thus some technical support for this ethical concern of ‘meddling with what we don’t understand”. For example, Mormède (2005) in a review of the opportunities to use molecular genetics in breeding for behaviour states that “However, a major limit to these studies is the limited basic knowledge about psycho-biological dimensions underlying behavioural trait variability, and the availability of reliable and meaningful measures of these,”

In summary, we believe that this issue that we have discussed under the heading of ‘stoics’ represents a real ethical issue, where an illusion of improved welfare might mask a continuing underlying problem, such as thwarted motivation.

Conclusions and Animal Welfare Implications

We have argued that breeding to change behaviour offers potential for improving production and welfare. It is technically possible to do, although there are various practical issues that need to be addressed for successful implementation. Primarily there is a need for well-validated abbreviated methods of recording behaviour or its proxies. Economics as the key driver for breeders will always be a barrier to implementation of behavioural traits relating to non-economic welfare traits, although there are of course a number of win-win traits where there is less conflict between profit and welfare such as reducing neonatal mortality.

Ethical concerns over ‘meddling with nature’ when breeding for behaviour need to be considered. In particular the issues of unforeseen consequences of selection (for example due to antagonistic genetic correlations between traits) and the reduction of animal integrity or naturalness are important. In terms of naturalness, domesticated animals are already compromised in this regard, making clear-cut definitions difficult. Where the environment for which selection occurs is seen as ethically desirable (e.g. extensive, free-range), there may be fewer problems, but decisions over selection to change behaviour in intensive environments could involve balancing between opportunities to improve animal welfare and the risk of reduced animal integrity.

Our position is that the resulting animal welfare (animal feelings) is of paramount importance here. The specific concern that selection for behaviour could result in extremely docile “Zombies” may give rise to disagreement between those who like the authors of the present paper are mainly concerned about preventing welfare problems for the animals and those who care about animal integrity and see excessively docile animals as lacking something of significant value. Breeding for “Zombies” could be guarded against in a selection programme by ensuring that a variety of behaviours are recorded, and the genetic correlations among them and other breeding goals are understood. A more important concern is the issue of “stoical” animals where breeding against behavioural (or other) indicators of welfare could mask a problem without really solving it, unless great care is taken in identifying accurate measures of the underlying problem, which may not always be possible when unobservable mental states are the ultimate indicator of a problem.

Acknowledgments

SAC is supported by the Scottish Government.

References

AEBC 2002 Animals and Biotechnology, a report by the Agriculture and Environment Biotechnology Commission.

Albers GAA, Gray GD, Piper LR, Barker JSF, Lejambre LF and Barger IA 1987 The Genetics of Resistance and Resilience to Haemonchus-Contortus Infection in Young Merino Sheep. International Journal for Parasitology 17: 1355-1363

Appleby MC and Hughes BO 1991 Welfare of laying hens in cages and alternative systems: environmental, physical and behavioural aspects. World's Poultry Science Journal 47: 109-128

Australian Limousin Breeders Society 2009 Limousin Assurance Programme. http://www.limousin.com.au/assurance-program.html .

Banner M 1995 Report of the Committee to Consider the Ethical Implications of Emerging Technologies in the Breeding of Farm Animals. London: HMSO, Ministry of Agriculture, Fisheries and Food.

Beilharz RG and Cox DF 1967 Genetic analysis of open field behavior in swine. Journal of Animal Science 26: 988-990

Bergsma R, Kanis E, Knol EF and Bijma P 2008 The contribution of social effects to heritable variation in finishing traits of domestic pigs (Sus scrofa). Genetics 178: 1559-1570

Bijma P, Muir WA and van Arendonk JAM 2007a Multilevel selection 1: Quantitative genetics of inheritance and response to selection. Genetics 175: 277-288

Bijma P, Muir WM, Ellen ED, Wolf JB and van Arendonk JAM 2007b Multilevel selection 2: Estimating the genetic parameters determining inheritance and response to selection. Genetics 175: 289-299

Boissy A, Fisher AD, Bouix J, Hinch GN and Le Neindre P 2005 Genetics of fear in ruminant livestock. Livestock Production Science 93: 23-32

Brascamp EW, Smith C and Guy DR 1985 Derivation of Economic Weights from Profit Equations. Animal Production 40: 175-180

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

Breuer KB, Beattie VE, Dunne LM, Slade EC, Davies Z, Mercer JT, Rance KA, Sneddon IA, Sutcliffe MEM and Edwards SA 2001 Validation and development of a behavioural test to predict the predisposition of growing pigs to perform harmful social behaviour such as tail biting.pp. 50 BSAS Scarborough,

British Limousin Cattle Society 2009 Limousin Society to Introduce Docility Scoring. http://www.limousin.co.uk/projects/docility_scoring.html .

Buitenhuis AJ and Kjaer JB 2008 Long term selection for reduced or increased pecking behaviour in laying hens. Worlds Poultry Science Journal 64: 477-487

Burrow HM 1997 Measurements of temperament and their relationships with performance traits in beef cattle. Animal Breeding Abstracts 65: 477-495

Canario L, Bergsma R, D'Eath RB, Lawrence AB, Roehe R, Lundeheim N, Rydhmer L, Knol E and Turner SP 2008 Genetic relations between the group effect for average daily gain, and post-mixing aggression and skin lesions in Swedish pigs. 200.Vilnius, Lithuania, Proceedings of the 59th Annual Meeting of the European Association for Animal Production.

Christensen LG 1998 Possibilities for genetic improvement of disease resistance, functional traits and animal welfare. Acta Agriculturae Scandinavica Section A- Animal Science Suppl 29: 77-89

Conington J, Collins J and Dwyer CM 2009 Breeding for easier managed sheep. Animal Welfare this issue:

Cooper MD and Wrathall JHM 2009 Assurance schemes as a tool to tackle genetic welfare problems in broilers. Animal Welfare this issue:

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 and Muir WM 1993 Selection for Reduction of Beak-Inflicted Injuries Among Caged Hens. Poultry Science 72: 411-420

Craig JV, Ortman LL and Guhl AM 1965 Genetic selection for social dominance ability in chickens. Animal Behaviour 13: 114-131

D'Eath RB, Roehe R, Turner SP, Ison SH, Farish M, Jack MC and Lawrence AB 2009 Genetics of animal temperament: aggressive behaviour at mixing is genetically associated with the response to handling in pigs. Animal in press:

Dekkers JCM and Gibson JP 1998 Applying breeding objectives to dairy cattle improvement. Journal of Dairy Science 81: 19-35

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

Duncan IJH and Filshie JH 1980 The use of radio telemetry devices to measure temperature and heart rate in domestic fowl. In: CJ Amlaner & DW Macdonald (eds) A Handbook on Biotelemetry and Radio Tracking pp. 579-588 Pergamon Oxford,

Ellenberg U, Mattern T, Seddon PJ and Jorquera GL 2006 Physiological and reproductive consequences of human disturbance in Humboldt penguins: The need for species-specific visitor management. Biological Conservation 133: 95-106

Faure JM and Mills AD 1998 Improving the Adaptability of Animals by Selection. In: T Grandin (ed) Genetics and the Behavior of Domestic Animals pp. 235-264 Academic Press San Diego,

FAWC 2004 Report on the Welfare implications of Animal Breeding and Breeding Technologies in Commercial Agriculture. London, Farm Animal Welfare Council. 2004.

Finn DA, Rutledge-Gorman MT and Crabbe JC 2003 Genetic animal models of anxiety. Neurogenetics 4: 109-135

Fraser D, Weary DM, Pajor EA and Milligan BN 1997 A scientific conception of animal welfare that reflects ethical concerns. Animal Welfare 6: 187-205

Grandinson K 2005 Genetic background of maternal behaviour and its relation to offspring survival. Livestock Production Science 93: 43-50

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

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

Hansen CPB 1993a Stereotypies in Ranch Mink - the Effect of Genes, Litter Size and Neighbors. Behavioural Processes 29: 165-178

Hansen SW 1993b Selection for behavioural characteristics in mink and the effect on reproduction results. *Genetics, Breeding and Reproduction of Fur Animals, NJF Report No 90, Proceedings of a NJFworkshop, Viborg, Denmark* 29 *April* pp. 35-41 Scandinavian Association of Agricultural Scientists (NJF) Viborg, Denmark,

Hazel LN 1943 The genetic basis for constructing selection indexes. Genetics 28, 476-490.

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

Holmes ND 2007 Comparing king, gentoo, and royal penguin responses to pedestrian visitation. Journal of Wildlife Management 71: 2575-2582

Irish Limousin Cattle Society 2009 Irish Limousin Docility Reaching New Heights. http://www.irishlimousin.com/docilityfile.html .

Jeppesen LL, Heller KE and Bildsoe A 2004 Stereotypies in female farm mink (Mustela vison) may be genetically transmitted and associated with higher fertility due to effects on body weight. Applied Animal Behaviour Science 86: 137-143

Jones RB and Hocking PM 1999 Genetic selection for poultry behaviour: Big bad wolf or friend in need? Animal Welfare 8: 343-359

Kadel MJ, Johnston DJ, Burrow HM, Graser HU and Ferguson DM 2006 Genetics of flight time and other measures of temperament and their value as selection criteria for improving meat quality traits in tropically adapted breeds of beef cattle. Australian Journal of Agricultural Research 57: 1029-1035

Kanis E, De Greef KH, Hiemstra A and van Arendonk JAM 2005 Breeding for societally important traits in pigs. Journal of Animal Science 83: 948-957

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

Kjaer JB and Sorensen P 1997 Feather pecking behaviour in White Leghorns, a genetic study. British Poultry Science 38: 333-341

Lambe NR, Conington J, Bishop SC, Waterhouse A and Simm G 2001 A genetic analysis of maternal behaviour score in Scottish Blackface sheep. Animal Science 72: 415-425

Lawrence AB, Conington J and Simm G 2004 Breeding and animal welfare: practical and theoretical advantages of multi-trait selection. Animal Welfare 13: S191-S196

Lawrence AB, Pryce JE and Simm G 2001 G x EEE: the missing link when breeding for welfare. In: JP Garner, JA Mench & SP Heekin (eds)pp. 90 Center for Animal Welfare UC Davis Davis, USA,

Le Neindre P, Trillat G, Sapa J, Menissier F, Bonnet JN and Chupin JM 1995 Individual-Differences in Docility in Limousin Cattle. Journal of Animal Science 73: 2249-2253

Løvendahl P, Damgaard LH, Nielsen BL, Thodberg K, Su GS 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

Macfarlane JM, Matheson SM and Dwyer CM 2009 Genetic parameters for birth difficulty, lamb vigour and lamb sucking ability in suffolk sheep. Animal Welfare .

Macnaghten P 2004 Animals in their nature: A case study on public attitudes to animals, genetic modification and 'nature'. Sociology-the Journal of the British Sociological Association 38: 533-551

Malmkvist J and Hansen SW 2001 The welfare of farmed mink (Mustela vison) in relation to behavioural selection: A review. Animal Welfare 10: 41-52

Mason G, Clubb R, Latham N and Vickery S 2007 Why and how should we use environmental enrichment to tackle stereotypic behaviour? Applied Animal Behaviour Science 102: 163-188

Mason G and Latham N 2004 Can't stop, won't stop: Is stereotypy a reliable animal welfare indicator. Animal Welfare 13: S57-S69

McInerney J 2004 Animal welfare, economics and policy. Report on a study undertaken for the Farm & Animal Health Economics Division of Defra.

Miczek KA, Maxson SC, Fish EW and Faccidomo S 2001 Aggressive behavioral phenotypes in mice. Behavioural Brain Research 125: 167-181

Mignon-Grasteau S, Boissy A, Bouix J, Faure JM, Fisher AD, Hinch GN, Jensen P, Le Neindre P, Mormede P, Prunet P, Vandeputte M and Beaumont C 2005 Genetics of adaptation and domestication in livestock. Livestock Production Science 93: 3-14

Mill JS 1863 Utilitarianism. Longmans, Green, Reader, and Dyer: London

Mills AD, Duncan IJH, Slee GS and Clark JSB 1985a Heart-Rate and Laying Behavior in 2 Strains of Domestic Chicken. Physiology & Behavior 35: 145-147

Mills AD 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

Mills AD, Woodgush DGM and Hughes BO 1985b Genetic-Analysis of Strain Differences in Pre-Laying Behavior in Battery Cages. British Poultry Science 26: 187-197

Mormède P 2005 Molecular genetics of behaviour: research strategies and perspectives for animal production. Livestock Production Science 93: 15-21

Muir WM and Craig JV 1998 Improving animal well-being through genetic selection. Poultry Science 77: 1781-1788

Neeteson-van Nieuwenhoven AM, Merks J, Bagnato A and Liinamo AE 2006 Sustainable transparent farm animal breeding and reproduction. Livestock Science 103: 282-291

Nielsen HM and Amer PR 2007 An approach to derive economic weights in breeding objectives using partial profile choice experiments. Animal 1: 1254-1262

Nielsen HM, Christensen LG and Odegard J 2006 A method to define breeding goals for sustainable dairy cattle production. Journal of Dairy Science 89: 3615-3625

Nielsen UL and Therkildsen N 1995 Selektionsforsøg for og imod pelsgnav hos mink. In: N Therkildsen (ed) *Faglig Årsberetning* 1993/94 pp. 209 Pelsdyrerhvervets Forsøgs - og Rådgivningsvirksomhed *A/S:* Holsterbro, Denmark,

Nimon AJ, Schroter RC and Stonehouse B 1995 Heart-Rate of Disturbed Penguins. Nature 374: 415

Olesen I, Groen AF and Gjerde B 2000 Definition of animal breeding goals for sustainable production systems. Journal of Animal Science 78: 570-582

Olsson IAS, Gamborg C and Sandoe P 2006 Taking ethics into account in farm animal breeding: What can the breeding companies achieve? Journal of Agricultural & Environmental Ethics 19: 37-46

Phocas F, Boivin X, Sapa J, Trillat G, Boissy A and Le Neindre P 2006 Genetic correlations between temperament and breeding traits in Limousin heifers. Animal Science 82: 805-811

Price EO 1984 Behavioral aspects of animal domestication. The Quarterly Review of Biology 59: 1-32

Pryce JE, Coffey MP and Brotherstone S 2000 The genetic relationship between calving interval, body condition score and linear type and management traits in registered Holsteins. Journal of Dairy Science 83: 2664-2671

Pryce JE, Conington J, Sørensen P, Kelly HRC and Rydhmer L 2004 Breeding Strategies for Organic Livestock. In: M Vaarst, S Roderick, V Lund & W Lockeretz (eds) Animal Health and Welfare in Organic Agriculture pp. 357-388 CABI Wallingford, UK,

Pryce JE, Esslemont RJ, Thompson R, Veerkamp RF, Kossaibati MA and Simm G 1998 Estimation of genetic parameters using health, fertility and production data from a management recording system for dairy cattle. Animal Science 66: 577-584

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

Rauw 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

Reif A and Lesch KP 2003 Toward a molecular architecture of personality. Behavioural Brain Research 139: 1-20

Rodenburg TB, Bijma P, Ellen ED, Bergsma R, de Vries S, Bolhuis JE, Kemp B and van Arendonk JAM 2009 Breeding amiable animals? Improving farm animal welfare by including social effects into the genetic model. Animal Welfare this issue:

Rodenburg TB, Buitenhuis AJ, Ask B, Uitdehaag KA, Koene P, van der Poel JJ and Bovenhuis H 2003 Heritability of feather pecking and open-field response of laying hens at two different ages. Poultry Science 82: 861-867

Rollin BE 2002 An ethicist's commentary on equating productivity and welfare. Canadian Veterinary Journal 43[2], 83.

Sandøe P 1996 Animal and human welfare - are they the same kind of thing? Acta Agriculturae Scandinavica Section A Suppl 27: 11-15

Sandøe P, Nielsen BL, Christensen LG and Sorensen P 1999 Staying good while playing god- The ethics of breeding farm animals. Animal Welfare 8: 313-328

Siipi H 2008 Dimensions of naturalness. Ethics & the Environment 13: 71-103

Silva B, Gonzalo A and Canon J 2006 Genetic parameters of aggressiveness, ferocity and mobility in the fighting bull breed. Animal Research 55: 65-70

Simm G 1998 Genetic Improvement of Cattle and Sheep. Farming Press: Ipswich, U.K.

Statham PTE, Green LE and Mendl M 2006 Development of a propensity to chew test as a predictor of tail-biting in pigs. Bristol, U.K.,

Su G, Lund MS and Sorensen D 2007 Selection for litter size at day five to improve litter size at weaning and piglet survival rate. Journal of Animal Science 85: 1385-1392

Svendsen PM, Hansen BK, Malmkvist J, Hansen SW, Palme R and Jeppesen LL 2007 Selection against stereotypic behaviour may have contradictory consequences for the welfare of farm mink (Mustela vison). Applied Animal Behaviour Science 107: 110-119

T-AP 1995 Standing committee of the european convention for the protection of animals kept for farming purposes (T-AP): Recommendations concerning Domestic Fowl (Gallus gallus).

T-AP 1999 Standing committee of the european convention for the protection of animals kept for farming purposes (T-AP): Recommendations concerning fur animals.

T-AP 2005a Standing committee of the european convention for the protection of animals kept for farming purposes (T-AP). Recommendations concerning pigs.

T-AP 2005b Standing committee of the european convention for the protection of animals kept for farming purposes (T-AP): Recommendations concerning farmed fish.

Turner SP, D'Eath RB, Roehe R and Lawrence AB 2009a Selection against pig aggressiveness at re-grouping; practical application and implications for long-term behavioural patterns. Animal Welfare this issue:

Turner SP, Farnworth MJ, White IMS, Brotherstone S, Mendl M, Knap P, Penny P and Lawrence AB 2006a The accumulation of skin lesions and their use as a predictor of individual aggressiveness in pigs. Applied Animal Behaviour Science 96: 245-259

Turner SP and Lawrence AB 2007 Relationship between maternal defensive aggression, fear of handling and other maternal care traits in beef cows. Livestock Science 106: 182-188

Turner SP, Roehe R, D'Eath RB, Ison SH, Farish M, Jack MC, Lundeheim N, Rydhmer L and Lawrence AB 2009b Genetic validation of skin injuries in pigs as an indicator of post-mixing aggressiveness and the relationship with aggression under stable social conditions. Journal of Animal Science in press:

Turner SP, Roehe R, Mekkawy W, Farnworth MJ, Knap PW and Lawrence AB 2008 Bayesian analysis of genetic associations of skin lesions and behavioural traits to identify genetic components of individual aggressiveness in pigs. Behavior Genetics 38: 67-75

Turner SP, White IMS, Brotherstone S, Farnworth MJ, Knap PW, Penny P, Mendl M and Lawrence AB 2006b Heritability of post-mixing aggressiveness in grower-stage pigs and the relationship between aggressiveness and production traits. Animal Science 82: 615-620

Van Oers K, de Jong G, Van Noordwijk AJ, Kempenaers B and Drent PJ 2005 Contribution of genetics to the study of animal personalities: a review of case studies. Behaviour 142: 1185-1206

Vinke CM, Eenkhoorn NC, Netto WJ, Fermont PCJ and Spruijt BM 2002 Stereotypic behaviour and tail biting in farmed mink (Mustela vison) in a new housing system. Animal Welfare 11: 231-245

Wolf BT, McBride SD, Lewis RM, Davies MH and Haresign W 2008 Estimates of the genetic parameters and repeatability of behavioural traits of sheep in an arena test. Applied Animal Behaviour Science 112: 68-80

Behaviour		Poultry	Pigs	Sheep	Cattle	Fur animals
Social	**Aggression**	Selection line studies (Craig et al 1965)	0.17-0.46 (Løvendahl et al 2005; Turner et al 2006b; Turner et al 2008; Turner et al 2009b)		0.28-0.36 (Silva et al 2006)	
	Sociality	Selection line studies (Mills & Faure 1991)		0.02 – 0.39* (Wolf et al 2008)		
Abnormal	**Damaging conspecifics**	Feather pecking 0.11-0.38 (Kjaer & Sorensen 1997; Rodenburg et al 2003); Selection line studies (Craig & Muir 1993; Buitenhuis & Kjaer 2008)	Tail biting 0.05 (Breuer et al 2005)			Fur chewing 0.30 (Nielsen & Therkildsen 1995; cited by Malmkvist & Hansen 2001)
	Stereotypy	Selection line studies (Mills et al 1985b)				Selection line studies (Hansen 1993a; Jeppesen et al 2004)
Fear	**of humans/ handling ease**	0.08 – 0.34 (Craig & Muir 1989); Tonic immobility selection line studies (Faure & Mills 1998)	0.38 (Hemsworth et al 1990) 0.03 – 0.17 (D'Eath et al 2009)	0.02 – 0.39* (Wolf et al 2008)	0.06-0.44 (Beef, Le Neindre et al 1995; Phocas et al 2006; Kadel et al 2006)	0.38 (Hansen 1993b; cited by, Malmkvist & Hansen 2001)

					0.07 (Dairy, Pryce et al 2000)
	of novel objects or places	tonic immobility selection lines (Mills & Faure 1991); Open field 0.10 – 0.49 (Rodenburg et al 2003)	0.16 (Beilharz & Cox 1967)		
Reproductive	**Maternal behaviour**		0.01-0.08 (Grandinson et al 2003; Løvendahl et al 2005)	0.13 (Lambe et al 2001)	0.06 – 0.09 (defensive aggression, reviewed by Burrow 1997)

Table 1: Examples of evidence for a genetic component of behaviour traits in farm animals. Evidence of successful selection experiments or estimates of heritability (h^2) from pedigree studies are given. Where a range of values is reported, this reflects both the use of multiple variables or test ages within one study, and differences across studies. *This study is difficult to classify as it recorded behaviour in a test of conflicting motivations (avoid a human vs. seek flock mates).