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Animal Welfare 2010, 19(S): 17-27
ISSN 0962-7286

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

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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 exist to increase the inclusion of behaviour in breeding indices. On a technical level, breeding for behaviour presents a number of 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 certain 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 unreactive ('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* 2010). 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 percentage, carcase 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 (eg T-AP 1995, 1999, 2005a,b), 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 a number of 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.

There are some limitations on livestock breeders. Selection from too small a number of parent stock can limit the gene pool leading to problems such as inbreeding depression, and this must be limited by breeding programme design (Villanueva *et al* 2006). Another limitation that might be expected is that selection would quickly use up all the available variability in a trait resulting in a relatively uniform population. In fact, practical experience shows that after many generations of selection, the availability of variation to select from is undiminished (Hill 2010). Since every trait results from an interaction between genes and the environment, it is possible that selection in a certain environment could result in animals that only perform well in that environment. For example, dairy cows bred for high milk yield in high-input systems might perform poorly in lower input systems, although in this particular example, increased yields are often realised across a range of systems (eg Jenet *et al* 2004).

Research into selection for behaviour

Behaviour is much more affected than physical traits by environmental influences, either at the time (eg presence of group-mates or humans) or in advance of behaviour (eg 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 (eg 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; Falconer & Mackay 1996), suggesting that selection for behaviour would be possible in principle.

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) or stress reactivity (Mormède 2005), or to increase 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,b; Rodenburg *et al* 2010). 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

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.

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, 2008, 2009)	–	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) 0.07 (Dairy, Pryce *et al* 2000)	0.38 (Hansen 1993b; cited by Malmkvist & Hansen 2001)
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)	–

* This study is difficult to classify as it recorded behaviour in a test of conflicting motivations (avoid a human vs seek flock mates).

methodology can be assumed but as yet has not been studied in great 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* 2010).

Genetic selection for farm animal behaviour in practice

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 Dutch mink 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 as a criterion for genetic selection by the Limousin breed societies in Ireland and Australia and is now being introduced in Britain (Australian Limousin Breeders Society 2009; British Limousin Cattle Society 2009; Irish 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).

The quality of maternal behaviour in sheep in response to her lamb (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). This trait is somewhat complex in that it depends mainly on the behaviour of the ewe, but also on the response of the lamb to handling for tagging (eg vocalisations). As such, selection on such a trait might result in changes in either or both ewe and lamb behaviour. Efforts to improve this trait 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* 2010).

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 in the context of scientific research, but are often prohibitive for practical implementation. To reduce these costs, quick behavioural tests (eg 'stick' test in mink; Malmkvist & Hansen 2001), automated measurement (eg flight speed from a crush in beef cattle; Burrow 1997) or proxy traits (eg skin lesion number as a proxy for aggressive behaviour; Turner *et al* 2006a, 2009, 2010) 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 (eg 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 (eg 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 (eg Breuer *et al* 2001; Statham *et al* 2006). As far as is possible, standardisation of the test situation is crucial during behavioural testing, otherwise absence of a behaviour might result from the lack of appropriate eliciting cues, rather than a reduced propensity of the animal to respond.

There may, however, be unintended consequences of using proxy measures, due to the complex nature of behavioural traits. For example, breeding for docile cattle has involved different methodologies in different countries, which is likely to result in different outcomes. The use of a more indirect proxy measurement, such as slow flight speed from a crush in the hope of selecting calm animals, might result in animals which were slow for another reason (eg because they were lame), or the response may not generalise as well as hoped to other situations. Breeding for few skin lesions 24 h after mixing to reduce aggression in pigs could result in blunt teeth, or reduced general activity rather than less fighting. Selection for groups of chickens that survive and produce eggs despite being beak-trimmed could similarly come about due to any number of mechanisms: selection could act to reduce cannibalistic behaviour, or to enhance the survivability or avoidance of damage in recipients, or it could make some feature of the recipients (such as the feathers) less attractive as targets.

To avoid these sorts of problems, it is essential that geneticists and ethologists collaborate in these efforts, and that behaviour is studied using appropriately detailed ethological methods at each step of the breeding process to ensure that the effect of selection is properly understood. Importantly, 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 or 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 (eg beef or sheep). Poorly designed scoring systems for behaviour which rely on the subjective assessments of multiple scorers 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. In practice, even with these problems, behaviour traits are heritable albeit at a low level (eg Pryce *et al* 2000). Well-designed, research-based objective scoring systems (Macfarlane *et al* 2010) or (validated) use of automation (eg image analysis for feather scoring or skin-lesion scoring) provide potential solutions which would result in increased heritability of traits, improving the efficacy of selection.

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 aimed primarily 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 (eg 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 the UK's Farm Animal Welfare Council (FAWC 2004), AEBC (2002) and the EU's T-AP committee (eg T-AP 1995, 1999, 2005a,b), there is 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 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 for milk production traits alongside cow conformation, udder health, longevity, calving and fertility allowing farmers (to some extent) to make decisions about which traits to focus on when purchasing semen (eg http://www.dairyco.org.uk/farming-info-centre/breeding—genetics.aspx).

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 organisations 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 programmes require animals of a certain breed such as slow-growing broilers (Cooper & Wrathall 2010) 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). It should be expected that this feeling might be strongest 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 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 has sometimes happened when, for example, species of animals have been introduced by humans into new territories.

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 slightly 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). The underlying idea here seems to be that some properties are viewed as more essential to an animal breed or species than others. Here, behavioural properties may seem to be more essential than purely physiological properties such as disease resistance. For example, to breed a wolf to become more docile and playful seems to affect the 'wolfness of the wolf' more than breeding it to be resistant to an infectious disease. The distinctions drawn here are, of course, not based on natural science. Rather, they seem to be derived from ethical or cultural ideas of what are the essential properties of different species.

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? On the grounds of interfering where we do not adequately understand, it could be argued there are much greater risks when attempting to alter the animal rather than the environment. Changes made to the external environment are relatively 'safe', in that they are easy to describe and to reverse, and their effect on behaviour is easier to understand in comparison with changes made by breeding to change an animal's behaviour.

Concerns over animal naturalness or integrity are also at 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 would 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* 2010).

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, by 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 lesser 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 too easy a 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 unreactive 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). Further change in this direction could therefore 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* 2010).

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 of 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 there 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 the capacity to experience higher mental states, resulting in a higher level of needs and wants makes room for a richer and better life which has a greater value in its own right. 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 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 (eg high fearfulness could result in inactivity).

Whenever possible, direct examination of the source of the problem is important to prevent such undesired effect (eg Conington *et al* 2010). However, as illustrated by the discussion around the example provided by Mills and co-workers (Mills *et al* 1985a,b), 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 which show little behavioural reaction may show prolonged elevations in heart rate, suggesting that they experience an emotional response that may be indicative of poor welfare (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 (eg 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 welfare problem, such as thwarted motivation.

Animal welfare implications and conclusion

We have argued that breeding to change behaviour offers potential for improving production and welfare. It is technically possible, 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. Economic profitability for the producer, 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 (eg 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.

Acknowledgements

SAC is supported by the Rural and Environmental Research and Analysis Directorate of the Scottish Government.

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