The role of breeding and genetics in the welfare of farm animals

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Implications

This review will focus on the role of animal breeding and genetics in the welfare of animals and will highlight that:

• Past selection on a narrow range of production traits has had welfare impacts.
• New breeding tools could enhance the rate of undesirable change in correlated traits of welfare significance.
• These new breeding tools could, however, also facilitate selection deliberately aimed at improving welfare-relevant traits.

Key words: aggression, behavior, feather pecking, genomics, selection

Introduction

Domestication has shaped and continues to shape the characteristics of domestic animal species through artificial genetic selection. This has led to considerable differences both between and within domestic animal species, but also to a number of similarities: Domestic species tend to have a reduced brain size, increased reproduction and growth, decreased fearfulness, and increased social motivation compared with their wild counterparts (Jensen and Andersson, 2005). Domestication started thousands of years ago; however only in the past 50 to 60 years has intensive selection for increased meat and egg production taken place, resulting in large increases in productivity (Rauw et al., 1998). This intensive selection on increased productivity has contributed to a number of welfare issues, such as cardiovascular problems in broiler chickens. Since the early 1980s, awareness of these welfare issues and research to address them has been increasing [Moss, 1980; Craig, 1981; Curtis and Stricklin, 1991; see the discussion by Veissier et al. (2012) on welfare assessment in practice]. On the other hand, genetic selection can also be used to alleviate welfare problems in farm animals. This can be done by direct selection against undesired behaviors, such as aggression in pigs (Turner, 2011) or feather pecking in laying hens (Kjaer et al., 2001), but also by more general approaches, aiming to select for animals that are suitable for large-group housing (Rodenburg et al., 2010). Genomic tools hold great promise for enabling genetic selection for complex traits (Fulton, 2012), including behavioral traits. A principal aim of new breeding technologies is to advance the rate of genetic progress, and Schaeffer (2006) predicted that genomic selection could double the rate of genetic progress in dairy cattle. Genomic tools therefore also enhance the risk of greatly accelerating the rate of any undesirable changes in traits of welfare significance that are correlated to the trait under selection. Approaches where we adapt the animals by genetic selection should always be combined with approaches to optimize the environment of the animals. Welfare will probably play an important role in future breeding goals for domestic animals. For some species, welfare traits are already part of the breeding index (e.g., lameness in dairy cows and fecal egg count in sheep). This review will focus on the relationship between genetic selection and animal welfare, describing the genetic variation between and within species. Furthermore, we will focus on the effects of selection for increased productivity on animal welfare, as well as on innovative approaches to reduce welfare problems by means of genetic selection.

Differences and Similarities between Domestic Species

The domestic species vary greatly in the traits under selection, the selection intensity placed on these traits, and the application of breeding technologies to achieve this. The emergence of large pig and poultry breeding organizations and the use of synthetic hybrid crosses by these organizations coupled with the increasing use of genomic-estimated breeding values in these and the dairy sectors (Eggen, 2012) contrasts with the limited use made of estimated breeding values in the sheep industry, although this is also developing (Hayes et al., 2012). As a consequence, the amount of genetic progress that has been achieved in improving the species from its ancestral state is much greater in some species than in others. A number of reasons exist for this discrepancy, not least of which include industry fragmentation and the challenge of phenotyping traits for selection under extensive conditions. Thus, the intensity of selection has differed between livestock species or types and is likely to differ more in coming years. While there have been notable welfare consequences of past selection decisions in the extensively managed breeds, such as an increased lambing rate, which is likely to have contributed to a reduction in lamb survival and an increased frequency of dystocia in some breeds or crosses of beef cattle, breeding-related welfare challenges are most commonly associated with the highly selected poultry, dairy, and pig sectors. Widespread uptake of technologies such as electronic identification coupled with a need to meet food security demands may accelerate the rate of genetic change in extensive species, presenting both opportunities and risks for animal welfare.
Genetic Variation within Species: Breeds, Genetic Lines, and Hybrids

Within each domestic species, different breeds have been created or developed during the course of domestication. Breeds can be very similar, as in the commercial laying hen breeds, but also as different from each other as a Chihuahua and a Danish dog in the Canis lupus familiaris species. Breeds can be custom made to specific geographical areas, such as chicken breeds selected for tropical environments, or can be more of a generalist type, such as White Leghorn hens. Similarly, many sheep breeds that are now considered to be rare were originally selected for good performance in a specific, sometimes isolated, geographical area (e.g., the Shetland, Soay, or Herdwick breeds). With generalist-type sheep taking over the larger part of intensive sheep production, maintaining genetic diversity by conserving these traditional breeds has become a challenge (Taberlet et al., 2011). Another development in sheep breeding is the development of easy-care breeds that produce easy-lambing flocks that require minimum human care (Conington et al., 2010). Selecting for easy-care traits should result in more robust animals that are less dependent on human caretakers, which could be positive for sheep welfare, for example by reducing the risk of human intervention weakening the ewe-lamb bond. However, the selection itself should be closely monitored to prevent major welfare issues as could occur during the transition period to an easy-care state when inspection and human intervention are deliberately minimized. Traditional breeds could play a role in developing these easy-care breeds, as they may be more suitable for this type of production than the generalist-type breeds.

In commercial breeding, traditional breeds play a minor role, and in many cases, high-yielding commercial crosses or hybrids are used. In pig and poultry production, purebred lines are used for genetic selection, and these are then crossed, frequently in a four-way cross to create the commercial hybrid product. In this way, complimentary characteristics of several lines are combined. The purebred lines are often highly inbred to increase homozygosity of alleles for specific traits and to maximise heterosis, which generally leads to improved performance in the offspring. To create these crosses, usually the first cross is made in the grandparent stock and the second in the parent stock. This method also allows one to use specialized lines for reproductive traits or for high yield in other traits: In broilers and pigs, the female lines are usually selected on reproductive traits and the male lines on fast growth rates and improved carcass conformation and feed conversion efficiency. The breeding programs are then evaluated by studying performance of the hybrid crosses. In sheep, low-maintenance breeds derived from upland flocks with good maternal characteristics are mated to less hardy, but more productive terminal sire breeds to produce crossbreds for fattening on lower ground (Amer et al., 2007).

Effects of Breeding for Increased Productivity on Animal Welfare

Breeding for increased productivity over the past 50 to 60 years has been very successful in terms of increased growth rate, milk yield, and egg production; however, it has also had negative consequences on behavior and welfare (Rauw et al., 1998). For this, the broiler chicken provides a clear example: Here, selection on increased growth for the past 50 years has been extremely successful, increasing growth rate from 25 to 100 g per day (Knowles et al., 2008). This success, however, comes at the cost of increased incidences of lameness, ascites, and sudden death syndrome (Bessei, 2006). Nielsen et al. (2003) showed that many of these welfare issues can be solved by using slower-growing broiler hybrids that grow to slaughter weight in eight instead of six weeks. In dairy cows, selection for increased milk yield has resulted in decreased fertility and longevity, increased leg and metabolic problems, and a greater incidence of mastitis and other diseases (Ottenacu and Broom, 2010). An effort is needed here to collect data on these welfare-related traits on-farm and to use this information in future breeding programs for dairy cows. Here, automatic data collection at an individual level, in or around the milking parlor, will play a pivotal role in the ability to address these welfare issues (Kamphuis et al., 2010). Where data are available, the broadening of breeding goals to include health and welfare traits has been shown to benefit economic return and, as such, these breeding goals have been adopted by some national dairy genetic evaluation systems (Wall et al., 2010). There are also examples where selection for increased production may have led to an increase in undesirable behavior: For example, tail biting in pigs has been shown to be correlated with genetic selection for lean meat (Breuer et al., 2005) and feather pecking in laying hens with early sexual maturation (Jensen et al., 2005). Behavior and welfare traits are starting to play a more important role in breeding programs in general. This is related to the fact that an increasing proportion of farm animals are kept in group housing systems, where behavior of individual animals has an impact on the performance of the whole group. For such systems to be successful, genetic selection should focus on successful groups rather than, or as well as, successful individuals (Cheng, 2010).

Breeding for Improved Animal Welfare

Selection experiments have shown that it is feasible to directly select against undesirable behaviors, such as feather pecking in laying hens (Kjaer et al., 2001) when all available selection pressure is placed on this trait. This type of approach has been very helpful in better understanding these behavioral problems and has allowed study of the underlying mechanisms. However, this approach would not be considered in commercial breeding where the majority of selection pressure is likely to remain on traits with a direct and quantifiable market value. Traditionally, breeding companies have focused on selection for individual production. However, with the development of group housing systems for most domestic animal species, this approach has to be reconsidered: The animal with the best individual performance may be harmful for the performance of the group, for instance, because this animal is very aggressive or shows increased levels of damaging behavior. Muir (1996) showed that by selecting on group performance rather than on individual performance, it is feasible to reduce mortality due to cannibalism in laying hens. More recently, Muir (2005) showed that the method was equally effective in reducing aggression and increasing growth rate in Japanese quail, while individual selection on the same trait resulted in the opposite outcome. Muir (2005) and Bijma et al. (2007) have developed new theoretical and statistical tools to quantify the heritable effects that animals have on their group mates. The first studies estimating these social genetic effects in commercial populations of pigs (Bergsmo et al., 2008) and laying hens (Ellen et al., 2008), indicate large heritable social effects: in laying hens, the heritability for the trait “survival” increased from 7 to 19% due to heritable social effects (Ellen et al., 2008). This indicates that including social effects in...
Reducing Damaging Behavior in Laying Hens

Performance of laying hens in group housing is strongly affected by social interactions: Behavioral problems such as feather pecking and cannibalism can result in high mortality levels, especially in large flocks in non-cage systems (Figure 1; Rodenburg et al., 2008). We know that feather pecking develops from foraging behavior (Blokhuis, 1986; Newberry et al., 2007). Foraging pecks probably develop into feather pecks in response to fear- and stress-inducing stimuli (Rodenburg et al., 2004): We found that chicks that were more fearful in an open field at a young age were more likely to develop feather pecking as adults than chicks that were less fearful at a young age. Ellen et al. (2007) started a selection experiment selecting on low mortality due to feather pecking and cannibalism in group-housed laying hens. Interestingly, birds selected for low mortality in group housing (performing less damaging pecking), were less fearful than birds from an unselected control line, even at a young age (Rodenburg et al., 2009). The exact mechanism of how foraging pecks develop into feather pecks in response to fear- and stress-inducing stimuli remains unknown. The serotonergic (5-HT) system may play a central role, as it is involved both in coping with fear and stress, foraging, feeding behavior, and in feather pecking (van Hierden et al., 2004). In birds selected for low mortality, we saw not only a reduction in fearfulness and stress sensitivity, but also changes in the peripheral serotonergic (5-HT) system (Bohluis et al., 2009). Importantly, associations have been found between feather pecking and genes involved in the serotonergic system (Flisikowski et al., 2009; Biscarini et al., 2010). Flisikowski et al. (2009), using high and low feather pecking selection lines, found an association between DEAF1, a gene for a regulatory factor of the serotonergic system, and feather pecking. Similarly, Biscarini et al. (2010) found an association between the gene for the serotonin receptor HTR2C and feather damage. This association was significant across a population of nine purebred selection lines.

There was a clear difference in allele frequency of this mutation between brown layers (35%) and white layers (84%; Figure 2, top panel; Biscarini et al., 2010). Furthermore, these results are consistent with results from these same birds of increased feather damage on the back and rump in white layers compared with brown layers (Figure 2, middle panel) and higher fearfulness in white layers compared with brown, which increased with age (Figure 2, bottom panel; Uitdehaag et al., 2008). If we would be able to further develop the genetic fingerprint associated with feather pecking in the future, this would greatly enhance our possibilities of selecting against this behavior in commercial breeding operations.

Breeding against Aggression in Pigs

Mixing pigs into new social groups is a routine procedure experienced several times during the life of most commercial pigs. This triggers aggression that can result in the accumulation of large numbers of superficial skin lesions (Figure 3), although pigs vary in the number of lesions they receive [range 1 to 140 (Turner et al., 2006a); interquartile range 26 to 114 [D’Eath et al., 2010]. Furthermore, aggressive behavior compromises the rate and efficiency of weight gain, meat quality, and carcass grading (D’Eath et al., 2010). Aggression can also heighten the risk of infection at a time when stress may suppress immune competence (Morrow-Tesch et al., 1994). Aggressive behavior is qualitatively the same in domestic pigs and their wild ancestors but is quantitatively heightened in duration and severity in the former (Stolba, 1988).

Retaining pigs in littermate groups without mixing from birth through to slaughter has proved difficult to achieve on-farm, in transport, and in lairage. Low-cost husbandry changes typically delay the onset of aggression without reducing its consequences or are difficult to integrate into routine management (Arey and Edwards, 1998). However, the option of selectively breeding against aggressiveness at regrouping is technically possible. Reciprocated fighting and the delivery of non-reciprocated bullying have moderate heritabilities in pigs (between 0.17 and 0.43), as does the number of resulting skin lesions (between 0.21 and 0.26; Lovendahl et al., 2005; Turner et al., 2006b, 2009). Furthermore, genetic correlations indicate that skin lesions can be used as an indicator of genetic propen-
sity to become involved in aggressive behavior, which would greatly ease the measurement of aggressive phenotypes for selection purposes (Turner et al., 2008, 2009). A beneficial genetic correlation ($r_g$) between 0.28 and 0.50; Turner et al., 2009) also suggests that selection to reduce aggression at mixing would reduce aggression in the weeks after group formation, suggesting that aggressiveness may be reduced in several contexts rather than that specifically in response to regrouping. Single nucleotide polymorphisms (SNPs) in a number of genes mediating the activity of the hypothalamic-pituitary-adrenal (HPA) axis, which comprises a fundamental neuroendocrine stress response pathway, have been implicated in the control of aggressiveness (vasopressin receptor 1B and glucocorticoid receptor; Murani et al., 2010). D’Eath et al. (2005) also reported differences between aggressive and unaggressive pigs in vasopressin and serotonin gene expression in certain regions of the brain. Furthermore, differential gene expression in the adrenals suggests that aggressive pigs display altered cholesterol metabolism and cell cycle activity comparable to that of unaggressive pigs.
to that achieved by exogenous stimulation with ACTH, a hormone mediating activity of the HPA axis (Murani et al., 2011). Selection against aggressiveness might therefore alter basic pathways that govern a range of biological functions. We have found that aggressive animals were also faster to enter the weighing scale at the end of the growing period (D‘Eath et al., 2009), although the implications of this correlation for animal welfare are difficult to derive. However, we did not find differences in general activity levels to underlie reduced aggressiveness. There also appears to be no genetic relationship between sow aggressiveness and maternal behavior (Lovendahl et al., 2005) and, using a modest dataset, between aggressiveness and either growth rate or back fat depth in grower-finisher pigs (Turner et al., 2006b). Selection on social genetic effects (Bijma et al., 2007) to favor pigs that have a heritable and beneficial effect on the productivity of group members was found by Canario et al. (2008) to alter aggressive phenotypes in favor of pigs that were aggressive at mixing but that rapidly established dominance relationships. These results were also confirmed in a different population of pigs (Rodenburg et al., 2010). This selection method could lead to a reduction of aggression under stable conditions and hence be positive for animal welfare.

Selection on social effects or genome-wide selection may ultimately avoid the need for routine phenotyping of aggressiveness, making it more feasible to reduce the expression of this behavior through selection.

Conclusion

Breeding and genetics has played and will continue to play an important role in the welfare of domestic animals. If genetic selection focuses only on increasing production of dairy, meat and eggs, there is a clear risk of increasing welfare problems related to high production levels, such as mastitis in dairy cows and cardiovascular diseases in broilers. A wider perspective is needed that encompasses both production and welfare traits, even though welfare may not be a primary breeding goal of the selection scheme. Here, the genomics era could offer opportunities to collect more precise information on the biological impact of certain breeding decisions. This could help breeders to make more informed choices in their selection programs. Genomic tools could also facilitate selection for complex behavioral and welfare traits, which are frequently impossible to measure on a large number of animals. Once the genetic fingerprint for such complex phenotypes is available, these welfare issues could be addressed by targeted genomic selection approaches.

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