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Breeding amiable animals? Improving farm animal welfare by including social effects in breeding programmes

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Abstract

Social interactions between individuals, such as co-operation and competition, are key factors in evolution by natural selection. As a consequence, evolutionary biologists have developed extensive theories to understand the consequences of social interactions for response to natural selection. Current genetic improvement programmes in animal husbandry, in contrast, largely ignore the implications of social interactions for the design of breeding programmes. Recently, we have developed theoretical and empirical tools to quantify the magnitude of heritable social effects, ie the heritable effects that animals have on their group mates' traits, in livestock populations, and to utilise those effects in genetic improvement programmes. Results in commercial populations of pigs and laying hens indicate large heritable social effects, and the potential to substantially increase responses to selection in traits affected by social interactions. In pigs, including social effects into the breeding programme affected aggressive behaviour, both at mixing and in stable groups, indicating changes in the way dominance relationships are established and in aggressiveness. In laying hens, we applied selection between kin-groups to reduce mortality due to cannibalistic pecking. This resulted in a considerable difference in mortality between the low mortality line and the unselected control line in the first generation (20 vs 30%). Furthermore, changes in behavioural and neurobiological responses to stress were detected in the low mortality line, pointing to reduced fearfulness and stress sensitivity. These first results indicate that including social effects into breeding programmes is a promising way to reduce negative social interactions in farm animals, and possibly to also increase positive social interactions, by breeding animals with better social skills.

Keywords: *animal welfare, genetic selection, group selection, laying hens, pigs, social behaviour*

Introduction

Social interactions among individuals, such as co-operation and competition, are key factors in evolution by natural selection. As a consequence, evolutionary biologists have developed extensive theories to understand the consequences of social interactions for response to natural selection. Results show that response to selection depends on whether interactions occur among kin or among unrelated individuals, and whether selection occurs at the individual level or at the group level. Other theoretical approaches have focused less on relatedness and more on the level of selection (individual or group selection), as the fitness of an animal also depends on characteristics of the group (Griffing 1967; Griffing 1976; Moore *et al* 1997; Bijma & Wade 2008).

Current genetic improvement programmes in agriculture, however, largely ignore the implications of social interactions for the design of breeding programmes (Muir 2005). At the same time, housing systems for farm animals are evolving to larger groups in which positive and negative social interactions have greater impact. Taken together, this strictly limits the possibilities of animal breeders to respond to welfare issues that are caused by negative social interactions in group-housed animals, such as cannibalism in laying hens, aggression in pigs and food competition in fish. A clear example of this has been described by Muir (2005), who used individual selection for increased bodyweight in group-housed Japanese quail (*Coturnix japonica*). After 25 generations of selection, there was no improvement in bodyweight. This was caused by the fact that individual selection for greater bodyweight resulted in a large increase in cumulative mortality at 6 weeks of age due to fighting and cannibalism (24% mortality versus 6% in the initial population). This example illustrates that individual selection in group-housed animals does not lead to traits that are optimal for the whole group, but instead may lead to increased negative social interactions.

Evolutionary theory for response to selection in the presence of social interactions provides a stepping stone for animal breeders to reduce negative social interactions and improve welfare by means of genetic selection. Recently, Muir (2005) and Bijma *et al* (2007a,b) have developed theoretical and empirical tools to quantify the magnitude of heritable social effects, ie the heritable effects that animals have on their group mates' traits, in livestock populations, and to utilise those effects in genetic improvement programmes.

Results in commercial populations of pigs (Bergsma *et al* 2008) and laying hens (Ellen *et al* 2008) indicate large heritable social effects. In growing pigs, social effects contributed substantially to the heritability estimates of growth rate and feed intake, indicating that pigs can have significant effects on growth rate and feed intake of their group mates (Bergsma *et al* 2008). Similarly, in laying hens, the total heritable variance for the trait survival increased from 7 to 19% due to heritable social effects (Ellen *et al* 2008). These results show clearly that including social effects in genetic improvement programmes has the potential to substantially increase responses to selection in traits affected by social interactions.

Here, we review the possibilities of including social effects in breeding programmes and discuss the effects of selection for improved social performance on animal behaviour, coping characteristics and animal welfare.

Group selection experiments

Previous studies have shown that the use of group selection methods can have marked effects on traits affected by social interactions, such as cannibalism in laying hens. Muir (1996) used group selection among sire family groups to select for survival in laying hens kept in battery cages. He did this by selecting successful groups with low levels of mortality due to cannibalism, rather than selecting successful individuals. Using this method, mortality was successfully reduced from 68% in generation 2 to 9% in generation 6. In generation 6, mortality in group housing was at a similar level as mortality in individual housing, indicating that cannibalism was no longer a major issue in group-housed birds. These changes in mortality were accompanied by changes in behaviour, stress physiology, and immunology (Cheng *et al* 2004; Cheng & Muir 2005). Under conditions of social stress, birds from the low mortality population were more hesitant to attack other birds, showed less feather pecking, had a lower H/L ratio and had lower dopamine and corticosterone blood concentrations, indicating lower stress levels (Cheng *et al* 2001; Cheng & Muir 2004). Cheng and Muir (2005) suggested that these changes in birds from the low mortality population may reflect a greater ability to cope with novel environments and to have a greater resistance to stressors than birds from the high mortality population.

It has to be stressed that, although the study by Muir (1996) produced interesting and important results, there are major ethical issues surrounding this type of experimental set-up: birds were not beak-trimmed and were kept under high stocking densities, which explains the initially very high mortality of 68% and there was no humane end-point for wounded birds (eg identifying cannibalistic birds earlier, removing them, and marking their whole group down as 'at risk' from the perspective of the next generation of group/family selection). Similar results could be obtained from studies with a more humane end-point. Other options may be to use models that can measure a bird's propensity to develop cannibalism, such as a Petri-dish filled with blood and covered with a membrane (Cloutier *et al* 2002).

The traditional method of group selection was clearly successful in reducing mortality due to cannibalism in laying hens. At the same time, changes were detected in the birds' ability to cope with challenges. Apart from ethical considerations, a drawback of this traditional method of group selection is that selection candidates need to be kept in groups, meaning that information on the performance of individual birds (egg number, egg quality) is not always available, making it a less attractive method for commercial breeders. Furthermore, by focusing selection on successful families, inbreeding may increase.

Selection on low mortality in group-housed laying hens

Following up on the work by Griffing (1967, 1976) and Muir (1996), Ellen *et al* (2007) developed a method that allowed inclusion of both individual selection for egg production and group selection for low mortality using selection between kin-groups. In brief, selection candidates were housed individually, allowing recording of individual egg production. The full siblings of these selection candidates were housed in family groups and in those groups mortality was recorded. Only selection candidates with low mortality levels in the group of siblings and sufficient individual egg production were selected for the low mortality line. In the control line, the standard commercial breeding programme was implemented, with a focus on individual egg production. This resulted in a considerable difference in mortality between the low mortality line and the control line in the first generation (20 vs 30%). Surprisingly, mortality in the second generation showed an erratic pattern, with large differences between repeated batches of the same line, and no systematic difference between the low mortality line and the control line. This indicates that traits such as cannibalism are very sensitive to environmental factors, such as management conditions. A way around this sensitivity to environmental factors may be to develop standardised tests to measure a bird's propensity to develop cannibalism. As mentioned before, Cloutier *et al* (2002) used a Petri-dish covered with a membrane to show that hens could learn to peck through this membrane and consume blood by social learning. Similarly, in pigs, a tail-chew test has been developed to predict an animal's propensity to develop tail biting (Breuer *et al* 2003). These tests may be useful for future studies.

To investigate the biological consequences of selection on social effects, we studied behavioural and physiological traits of these birds in the second generation of selection in various environments (Rodenburg *et al* 2008, 2009a,b;

Table 1 Mean (± SE) lesion scores on different body parts, post mixing and in a steady situation, for pigs with high and low social breeding value for growth (SBV; with a higher lesion score indicating more lesions).

Body part	Post mixing		Steady situation	
	High SBV	Low SBV	High SBV	Low SBV
Front	17.03 (± 0.98)	11.59 (± 0.84)**	4.27 (± 0.32)	4.77 (± 0.34)
Middle	7.80 (± 0.72)	7.46 (± 0.56)	1.94 (± 0.19)	2.33 (± 0.27)
Rear	1.95 (± 0.28)	2.10 (± 0.27)	0.90 (± 0.11)	1.28 (± 0.17)
Back	–	–	1.08 (± 0.17)	1.63 (± 0.24)*

* $P < 0.05$; ** $P < 0.01$.

Bolhuis *et al* 2009). It was found that selection for low mortality between kin-groups leads to animals that are less fearful and less sensitive to stressors in a range of behavioural tests. Consistent results have been found both in young chicks (Rodenburg *et al* 2009b) and in adult birds (Bolhuis *et al* 2009) in various environments (cages and floor pens). These results fit well with research from previous studies, where it was found that birds that were fearful at a young age, were more likely to develop damaging pecking behaviour as adults (Rodenburg *et al* 2004). Similarly, chicks from a low feather-pecking line were found to be more active in an open-field test than birds from a high feather-pecking line (Jones *et al* 1995). Birds selected for low mortality also had a decreased corticosterone response to manual restraint compared with control birds (Rodenburg *et al* 2009a), which is in accordance with the results of Kjaer and Guémené (2009), comparing high and low feather-pecking lines. Furthermore, line differences were found in peripheral serotonergic activity: birds from the low mortality line had higher whole-blood serotonin concentrations and a low platelet serotonin uptake (Bolhuis *et al* 2009). There are indications that peripheral (platelet) serotonergic activity may mirror brain serotonergic activity in humans and rodents (Bianchi *et al* 2002; Rausch *et al* 2005) and recently also in chickens (Uitdehaag *et al* submitted), which would provide us with a less invasive measure of serotonergic activity. In laying hens, brain serotonergic neurotransmission has been related to the predisposition of a bird to develop damaging behaviour (van Hierden *et al* 2004).

In summary, selection for low mortality in laying hens resulted in birds that are less fearful and less sensitive to stress and show changes in the serotonergic system, which is strongly involved in social behaviour, coping with fear and stress, exploration, and personality traits. Further research is needed to clarify the effects of selection for low mortality on behaviour and welfare traits, and to confirm the effectiveness of this method to reduce mortality in group-housed laying hens.

Selection on social breeding values in pigs

In pigs, an experiment was carried out where 12 groups of pigs with a high social breeding value (SBV) for growth were compared with 12 groups of pigs with a low SBV for growth, with group sizes ranging from eight to ten individuals (de Vries, unpublished results). Pigs with a high SBV for growth were expected to increase the growth rate of their group mates, whereas pigs with a low SBV were expected to decrease the growth rate of their group mates. We expected pigs with a high SBV to be less aggressive than pigs with a low SBV.

Selection for social effects affected aggressive behaviour: unexpectedly, pigs with a high SBV for growth had more lesions to the front of the body just after mixing (at four weeks of age) than pigs with a low SBV (Table 1; de Vries, unpublished results). Similar results were found by Canario *et al* (2010), using similar methods in a Swedish population of pigs. This indicates that pigs with a high SBV were involved more frequently and more vigorously in reciprocal fighting shortly after mixing (Turner *et al* 2006). At six weeks post mixing, however, pigs with a high SBV for growth had fewer lesions on the back, indicating less aggressive interactions under stable conditions, ie once the dominance hierarchy has been established (de Vries, unpublished results). It may be that as pigs with a high SBV spent more time fighting just after mixing, they had a more stable dominance hierarchy than groups of pigs with a low SBV. This may have reduced aggression under stable conditions in groups with a high SBV. Under stable conditions, mutual fighting rarely occurs (Bolhuis *et al* 2005a, 2006), rather, unilateral (series of) head knocks or bites are observed which can be elicited by competition, discomfort, annoyance, irritability or frustration (Arnone & Dantzer 1980; Hagelsø Giersing & Studnitz 1996). Apart from differences in the tendency to display aggression, groups of pigs with a high SBV may also differ in conditions that elicit aggression in their group mates. In contrast to the study by de Vries (unpublished results), Canario *et al* (2010) found that pigs with a high SBV for growth had more

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lesions under stable conditions. Interestingly, in their study, pigs were not separated in groups with high or low SBVs, but were mixed. One explanation for this difference between studies may be that in mixed groups, pigs with a high SBV for growth receive more bullying, hence they might benefit from being housed with pigs with similar personality traits. Of course, to test this hypothesis an experiment needs to be conducted with mixed and unmixed groups under similar environmental conditions, as the differences may also have been due to other factors, such as hybrid, level of aggression, pen size, etc.

Personality traits can have profound effects on group performance, as has previously been found in pigs by Hessing *et al* (1994). They characterised piglets using the back-test (Hessing *et al* 1993), as either high resisting (HR) or low resisting (LR) based on their response to manual restraint. Results showed that mixed groups of HR and LR pigs had a better group performance than groups consisting of only HR or only LR pigs (Hessing *et al* 1994). Bolhuis *et al* (2005b) also showed that HR and LR pigs differ considerably in their aggressive behaviour. They found that HR pigs showed more aggressive behaviour at mixing, but there was no difference in achieved social rank between HR and LR pigs. In LR pigs a relationship was found between self-initiated fights and social rank, whereas in HR pigs this was not the case. HR pigs showed high levels of aggression regardless of their success (Bolhuis *et al* 2005b) and were also more aggressive under stable conditions (Bolhuis *et al* 2005a, 2006). It may be that such individuals cause problems in social groups, because they have difficulty in adapting their strategy.

If aggression is the main problem limiting growth rate in groups of pigs, including an SBV for growth rate in the breeding programme may skew the distribution of personality types towards LR pigs. Alternatively, if other traits affect growth in group-housed pigs, for instance high levels of oral manipulation of pen mates, leading to restlessness and increased aggression, the distribution of personalities in the selected population may look completely different as LR pigs are more prone to manipulative behaviour than HR pigs (Bolhuis *et al* 2005a). It has to be stressed here that it is not yet known which 'social' factors are limiting growth rate in groups of pigs: apart from aggression and damaging behaviour, it may be other factors, such as reducing access to food or to warm resting areas, increasing group activity, disease transmission, etc.

Interestingly, in the study by de Vries (unpublished results), there was no difference in performance between the pigs selected for high or low SBVs for growth. Both populations had very high growth rates. It may be that in this case social interactions were not limiting performance, but it may also be that pigs benefited from being housed with pigs with similar individual characteristics. This seems to contradict the results from Hessing *et al* (1994), who found that mixed groups had the best performance, but both in groups with high and with low SBVs a mix of HR and LR pigs was found. Furthermore, large differences in behaviour between HR and LR pigs in the study by de Vries (unpublished results) confirm the importance of monitoring personality traits in group-housed pigs. Further research into this topic is being conducted at this moment.

In pigs, first results on inclusion of social effects into the breeding programme indicate that this leads to changes in aggressive behaviour. Pigs selected for high SBVs, expected to have a positive effect on the growth rate of their group mates, seemed to be more aggressive just after mixing, but less aggressive under stable conditions. Group composition may have marked effects on social behaviour and performance. It appears that in pigs (as well as in chickens) social breeding values are context-specific, and the nature of this should be further investigated.

Conclusion and animal welfare implications

We reviewed the possibilities of including social effects in breeding programmes and discussed the effects of selection for improved social performance on animal behaviour, coping characteristics and animal welfare. From a genetic perspective, including social effects in breeding programmes is expected to increase the selection response to selection on production traits, such as growth and feed intake, substantially (Bergsma *et al* 2008; Ellen *et al* 2008), indicating that social interactions can have a marked effect on animal performance. From the selection experiment in laying hens by Muir (1996) it becomes clear that group selection methods are powerful tools to reduce negative effects of social interactions on performance, such as cannibalism in laying hens. In laying hens, selection between kin-groups on low mortality affected behaviour, stress physiology and the serotonergic system (Bolhuis *et al* 2009; Rodenburg *et al* 2009a,b). These changes indicated that laying hens selected for low mortality are less fearful and less sensitive to stress than control birds and show changes in the serotonergic system. Our results were similar to the effects found in the lines selected by Muir (1996). Similarly, in pigs, including social effects for growth in the breeding programme resulted in changes in aggressive behaviour. Pigs selected for high SBVs, expected to have a positive effect on the growth rate of their group mates, seemed to be more aggressive just after mixing (de Vries, unpublished results; Canario *et al* 2010). Group composition may have marked effects on social behaviour and performance.

The response to selection has not always been clear-cut: in the laying hen experiment effects on mortality were not always consistent, when comparing the first and second generation of selection. This might be due to the fact that the development of cannibalism is very sensitive to environmental factors, such as management conditions. Similarly, in the selection experiment on pigs, there were no differences in performance between the pigs selected on high or low SBVs. These discrepancies will be studied further in the near future.

In conclusion, including social effects into breeding programmes seems a promising way to reduce negative social interactions in farm animals and, possibly, to also increase positive social interactions, by breeding animals with better social skills. This is expected to have major, positive effects on the welfare of group-housed animals.

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