

MODELING OF SOCIAL DOMINANCE WITH BINARY EXPRESSION ASSUMING SINGLE DOMINANT ANIMAL PER PEN

by

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(Under the Direction of Ignacy Misztal)

ABSTRACT

The objectives of this study were 1) to evaluate the effectiveness of the proposed method by Misztal and Rekaya (2007) in the case of binary expression of social dominance and to compare their findings with Muir and Schinckel (2002) and 2) to develop a Bayesian procedure for assignment of social dominant status for jointly penned animals. The effect of dominance advantage was only present in records of dominant animals and was a fixed value in Model 1, or equal to the effect of social dominance plus constant in Model 2. The estimate of the dominance advantage was unbiased when the covariance was 0, was biased upwards when the covariance was positive, and downwards if negative. The probability of identifying the true dominant animal in each pen was 0.31, 0.51, 0.75, and 0.85 when the dominance effect was 0.5, 1, 1.5, and 2 residual standard deviations, respectively.

INDEX WORDS: Social dominance, Bayesian, Associative effects.

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B.V.Sc & AH, Acharya N. G. Ranga Agricultural University, India, 2005

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment
of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2007

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DEDICATION

To my beloved parents and my sisters.

ACKNOWLEDGEMENTS

I would like to thank Dr. Ignacy Misztal for accepting me as a student. His meticulous guidance, constant encouragement and endless support are commendable. I place my deep sense of gratitude and thanks to Dr. Romdhane Rekaya for all his guidance support and thought provoking discussions. Also, I would like to thank Dr. Bertrand for his kind support. I would like to thank all the graduate students in animal breeding group at UGA. Finally, special thanks to my family and my friends at UGA.

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CHAPTER 1

INTRODUCTION

Animal welfare is an important concern in today's livestock industry. One factor of particular interest in animal welfare is competition among jointly penned animals. Competition among farm animals has a negative impact on the overall profitability of the farm. Further, aggressive interactions have many physical and physiological effects on farm animals. Warris and Brown (1985) reported that these interactions will reduce carcass quality in pigs, reduce feed intake, and lead to poor weight gains (Baxter, 1981; Hansen et al., 1982; Linderaman and Kornegay 1984; Meyer et al., 1984).

Competitive behavior is often expressed in antagonistic offense, defense, and submissive or escapes components (Petherick and Blackshaw, 1987). Aggressive interactions are a subset of agonistic behaviors which include contact behaviors and threats that are offensive in nature. With an evenly matched group, the heaviest animals tend to be the most aggressive and gain more weight. On the other hand, aggression was correlated with social dominance but not with weight in an unevenly matched group (Tindsley, 1984). Turner et al. (2001) suggested that domestic pigs under commercial conditions exhibit dyadic dominance relationships, and the number of dyadic relationships established increases linearly with the group size. Hughes et al. (1997) reported that the frequency of aggressive behaviors of laying hens in stable flocks of 700 was considerably less than the ones reported for smaller group sizes.

Competitive interactions can be accounted for during the selection process through the inclusion of a social dominance component in genetic evaluation models. Several theories for

addressing this issue have been developed over the years (Griffing, 1967, 1968a, 1968b, 1969, 1976a, 1976b). Falconer (1981) concluded that “competition is an important factor in plants, often making sib correlations largely meaningless, particularly with characters related to yield”. Wright (1977) postulated that in the presence of competitive effects, selection could result in a nonlinear response and progressively could become less effective until a plateau is reached, beyond which selection is detrimental. In aquaculture, selection for growth rate tends to favor more aggressive fish (Ruzzante & Doyle, 1991).

Muir and Schinckel (2002) and Muir (2005) have extended the classical genetic evaluation model to include competitive advantage effects in order to account for aggressive interactions. Van Vleck and Cassady (2003) used a competition model in a simulation study and reported a severe systematic bias as they were unable to recover the true parameters used in the simulation. Arango et al. (2005) concluded that estimating the variance components of competitive effects is difficult with small data sets and especially in a less competitive environment. Rutten et al. (2005) used a mixed model methodology to infer the presence of aggression in fish. Chen et al. (2005) concluded that when the pen effect and competitive effects are included in the statistical model, the competitive effects variance was small.

More recently, Misztal and Rekaya (2007) presented a new paradigm for inferring social dominance in a genetic model. They assumed that social dominance could be expressed nonlinearly. When only one animal per pen is assumed dominant, their model reduces to a special binary case where the dominant animal could either have a fixed advantage or varying (i.e., function of the breeding value) over its passive pen mates.

The objectives of the current study are:

1. To evaluate the effectiveness of the proposed method by Misztal and Rekaya (2007) in the case of binary expression of social dominance and to compare it with Muir and Schinckel (2002).
2. To develop a Bayesian procedure for assignment of social dominant status for jointly penned animals.

CHAPTER 2

REVIEW OF THE LITERATURE

Social Organization

Social organization in farm animals is well structured. In large herds, the practice of grouping animals increases frequent interactions among the animals and thereby causes instability in the hierarchy. Social dominance exhibited by animals in an organized hierarchy is assumed to be a quality possessed by each animal in its own distinct way (Powell, 1974) and exhibited in varying degrees. The hierarchies established by one group of animals or a particular animal depend on the prediction made about the course of future agonistic interactions or the outcomes of such competitive situations. Typically, animals form subgroups with an established social order when there is no scarcity for food. Factors responsible for maintaining the stability in a group include high population density within that group, space restrictions, and dominant subordinate interactions. In the dominant hierarchy, males are dominant over females and social dominance increases after castration; apparently older animals are dominant until physical activity is impaired. Further, dominance hierarchy is a learned process and the status of a subordinate animal would not alter even when the relative sizes are reversed with increasing growth. Animals with a winning history will always dominate others and new entrants into unfamiliar surroundings will subordinate the existing individuals (Blackshaw, 2003).

Agonistic behavior is any physical threat by any one animal that would reduce the freedom of others and is expressed in conflict situations as offense, defense, and submissive escape components (Petherick, 1987); agonistic behaviors are a function of interacting phenotypes.

Submission occurs whenever an animal does not attack and is expressed by the animal lying down, turning away, or being passive, whereas aggression includes threat, attack, and retreat and helps in establishing a stable hierarchy system creating losers and winners (Ewbank, 1972).

Evolution of Social Dominance

Studies on the evolution of social dominance provide a better insight into phenotypic interactions. Using an interacting phenotype model, Moore et al. (1997a) concluded that information on selection and inheritance are required for the complete understanding of the evolution of social dominance. Preferential access to resources is associated with high status in hierarchy (Wilson, 1975; Bernstein, 1981; Drews, 1993). West-Eberhard (1979) stated that “nonspecific rivals are an environmental contingency that can itself evolve”, inferring that social dominance is an emergent property with indirect genetic effects (Moore et al., 1997a). Selection and evolution of both interacting participants lead to evolution of social dominance when selection is based on both aggression and submission and with an extent as a function of interaction. Andersson (1994) investigated the relationship between dominance and selection and argued that dominance may result in male-male competition in sexual selection. Heritability of social behavior is difficult to compute in lieu of the inherent variability in social dominance (Fuller et al., 1976), but Jonsson (1985), studying pigs, found that dominant sons have dominant fathers.

Factors Responsible for Increased Aggression and Maintenance of Social Dominance

1. Food and Feeding Sites.

Possession of feeding sites is important in initiating aggression and, in the majority of cases, aggressive interactions are initiated by the subordinates (Baxter, 1981).

2. Space and Group Size.

Along with food, space is a major factor inciting aggression. This may be due to a large group size or poorly-established hierarchies. A large group is good for stability of social dominance but aggression develops if the individual in a pen does not recognize its pen mates. For example, Hughes et al. (1977) concluded that frequency of aggressive interactions in a stable flock of 700 or more laying hens was less than the frequency found in smaller flocks. In addition, there was a reduction in the frequency of interaction in pigs which were previously housed in large groups (McBride et al., 1964). This paradox can be explained by the modification of social structure in smaller groups which causes individual recognition to be less difficult.

3. Weight and Weight Asymmetry.

In pigs, body weight is the best indicator of potential for growth. Within an evenly matched group, the heaviest animals tend to be the most aggressive ones and also to show the most weight gain. On the other hand, in an unevenly matched group aggression was correlated with social dominance but not with weight (Tindsley, 1984). Andersson (1994) studied the relationship between weight asymmetry and aggression by mixing two unfamiliar groups from two different environments. Following game theory, it is hard for researchers to assess relative strength among evenly matched opponents. Large weight asymmetry within a group decreased the fighting duration when compared to groups that had smaller weight asymmetry because weight asymmetry would make smaller animals cease fighting quickly. Weight asymmetry for larger pigs increases an individual pig's chances of winning; at least 3 kg of weight difference between opponents was required for an animal to succeed in a confrontation.

4. Straw.

Straw reduces aggression in animals as it occupies the animal's time and has a calming effect (Hansen et al., 1980).

5. Pheromones

McGlone (1980) showed that agonistic behaviors are modulated by pheromones.

6. Sex.

Males are more dominant over females, indicating a difference in social dominance style between the sexes. Charlotte (2004) investigated this problem using the DomWorld model. According to this model, variation of social style difference lies in between two extremes: egalitarian societies and despotic societies. Indication of differences in the hierarchy system is a criterion to determine the dominance style. In an egalitarian society, a hierarchy is poorly developed with fellow mates sharing the benefits more or less the same, whereas a despotic society has a clear gradient in hierarchy where high-ranking animals receive more benefits than low-ranking animals. In a despotic society, males have a greater intensity of aggression and initial wins predominantly attributed to male-biased sexual dimorphism. Greater initial dominance and single events of either victory or defeat contribute to lesser differentiation in the hierarchy of males. Thus, males tend to create an egalitarian society while females are more likely to create a despotic society.

7. Learned Behavior.

A recent victory or defeat will affect subsequent attempts, leading to winner and loser effects (Chase et al., 1985). The future outcome of winning comes from past social experience in a site because winners tend to associate the site with dominating and winning. However, the losers' past experience would make them associate the site with stress and being dominated.

Asymmetry in this learning process was related to site-associated experience, explained by submissive individuals failing frequently in subsequent attempts (Sylvie et al., 1995).

8. Mixing Unfamiliar Animals

The mixing of unacquainted animals after weaning contributes to aggression in pigs. A simple linear type of hierarchy develops after mixing animals for the first time (McBride et al., 1964), within 1 h of mixing (Symoens et al., 1969), and establishes into social dominance after 24 to 48 h. Ewbank (1971) suggested that a pig at a lower hierarchy level returning into a group after 3 days was seen as a stranger by its pen mates.

9. Prior Residence Effect

The effect of prior residence and acquiring profitable feeding sites in juvenile Salmon was studied extensively by Huntingford et al. (1987), who classified the feeding sites as top, medium, and bottom in rank based on prior residence. An animal that arrives first to a specific area has a dominant advantage over subsequent animals that come to the same area (Archer, 1987; Huntingford, 1987; Krebs and Davies, 1987; Turner, 1987). Differential performance exhibited by individuals in varied competitive environments is congruent with each specific behavioral profile.

10. Social Hierarchies.

The merging of social hierarchies affects the dominance rank of individuals. Earley (2006) studied the concept of dominance rank in context-dependent situations and concluded that greater status is achieved by animals after merging from a perfusion group with dominant animals, and vice versa for subordinate animals. The dominant rank achieved by an individual greatly depends on the context e.g., familiar/unfamiliar surroundings, residence, and food (Bernstein, 1980; Nelissen, 1985; Cristol, 1990; Wiley, 1990; Chase, 2001). In spite of

familiarity with the dominant animals in a group, the movement of a low-ranking animal from one subgroup to another does not alter its status, contrary to evidence found from aviary studies (Wiley, 1990; Cristol, 1995a). In other words, rank stasis or equilibrium in subgroups is often achieved because of an ability to identify dominant opponents.

Physical and Physiological Effects of Social Dominance

Social dominance has a negative impact on the potential of the animal and thereby the productivity of the farm itself. Frequent antagonism may result in negative yield (Muir, 2002). Aggression also causes reduction of meat quality in pigs because of lacerations resulting from fighting (Warris, 1985). Experimental results on increased aggression with limited resources (food, water, space) showed there was both a substantial decrease in the feed conversion ratio and differential weight gain (Baxter, 1981; Hansen, 1982; Hsia, 1984; Lindemann, 1984). However, by minimizing agonistic interactions the performance and productivity of the animals will improve. Ewbank (1972) showed that an overall gain in feed efficiency can be achieved through the regrouping of unacquainted pigs. In addition, altering the design of a specific pen, by adding defined barriers between feeding and secure areas, is beneficial in the case of pigs. To maintain stability in social hierarchy, animals of the same group are to be retained from weaning to slaughter.

Social Dominance in Different Species

Social dominance is widely studied in different species that are of interest to commercial farming. Dominance relationships are unidirectional in the case of poultry and cattle (Beliharz et al., 1967). In small flocks of birds, relationships are transitive i.e., the dominant bird pecks all others; the second one pecks others except those on the top; and so on (Wood-Gush et al., 1955).

In large flocks, relationships are circular, and the birds will not accommodate rank relationships; therefore, once social dominance is fully established, there will be less aggressive attacks.

A quantitative score dominance value (DV), an expression of individual reaction to a particular environment, is used to evaluate an animal for social dominance (Siegel, 1960; Beilharz et al., 1963). The animal with the greatest DV is dominant and wins most of its fights. In pigs, the DV is genetically controlled and affects the weight of pigs at different levels of nutrition. Bride et al. (1960) concluded that relative rank and initial weight influenced initially on a pig's growth but rank is ultimately more important.

Social Dominance in Pigs.

The typical social structure of wild boars is composed of four sows centered with their litter mates (5 to 6 piglets) and maintained by non-aggressive interactions or by very low-aggressive behaviors (McGlone, 1986). The social structure of a free ranging pig is similar to the wild boar, composed of a small group of sows and their juvenile litter. Relatively less aggression in wild boars could be due to both the close relationship existing among them and a lack of competition for resources. Domestic pigs raised under commercial conditions exhibit dyadic relationships (Turner et al., 2001) which are stable in a flock of 10 to 30 and increase linearly with pen size. Aggression in newly-formed groups is most common due to unfamiliarity in the first instance and, later on, scarcity of resources. Short attack latency and long attack latency are two distinct categories of aggressiveness (Erhard. et al., 1997) and influence the strategies used for coping with social dominance. Active capers have short attack latency and vice versa. Erhard et al. (1997) explained that rank, immediacy to attack, and immediacy to approach trough are important variables that influenced aggressiveness in pigs.

Social Dominance in Poultry.

Social organization in poultry is varied within housing systems. In a cage system, pecking and threat behaviors help in establishing a definite hierarchy, which will take place just before 2 to 3 wk of laying. Agonistic pecking behavior in hens begins after hatching; it takes 6 to 8 wk for cockerels and 8 to 10 wk for pullets to obtain complete stability in a dominance hierarchy. Peck orders are not uncommon in cage and breeder sheds. In the case of broilers, it was shown that the peck order and social hierarchy are relatively unimportant (Siegel, 1984). This may be due to early processing of birds before reaching the age to establish hierarchy.

Laying hens show complex interrelationships with social rank, aggressiveness, and feeding behavior. Mench and Keeling (2001) argued that communication among these flocks takes place by signals (displays and vocalizations). Birds in large flocks recognize their mates and birds in overlapping territories by individual recognition, whereas hens can recognize breeds but not individuals within a breed. But Mauldin (1992) concluded that under commercial poultry conditions it is difficult for individuals to remember and recognize their flock mates. Territorial behavior is important in large flocks because it reduces the conflict between two strangers (McBride and Foenander, 1964). Birds spend most of their time in a territory where they are dominant and tend to live in neighborhoods that are familiar to them (Craig and Guhl, 1969).

Feeding behavior of laying hens shows specific patterns close to others with social attraction. Chickens peck more often when they are fed in groups compared to when they are fed individually. McBride (1963) showed that hens space their heads at regular patterns and avoid frontal confrontation while feeding. Further, Hughes and Wood-Gush (1967) stated that aggression is provoked by an approaching bird rather than one in close proximity. Most of the aggression takes place at feed troughs, making dominant animals more accessible to feed.

Al-Rawi and Craig (1975) conducted experiments on space restriction and aggressiveness in birds. They observed that after an initial decrease in space, interactions increased and decreased on further decrease of space. Specifically, individuals show less aggressive interactions in the presence of dominant animals because a lack of space for displaying threats results in a decrease in the amount of agonistic reactions, what is known as the third party effect (Ylando and Craig, 1980).

Social Dominance in Cattle

Cattle herds exhibit dominance hierarchies, the stability of which is influenced by age, weight, rank, and height at withers (McPhee, 1964). Reverse dominant hierarchy also exists in cattle; as the age increases, younger animals dominate the older cattle. Research has also found that smaller subgroups of dominant hierarchies may exist within a large group that has a linear hierarchy system in a ritualized sequence. Stricklin (1981) stated that dominance in cattle herds is an issue when there is competition for potential resources (food, water) and that further combats between the animals are reduced once the hierarchy is fully established.

Social Dominance in Fishes

In fish, the hierarchy system develops in intensive rearing farms. Aggressiveness is noticed when the dominant fish controls a territory for food resources. Fierce competition has proven to be the cause for mortality among the members of different families in Nile Tilapia during their early life (Giaquinto and Volapto, 1997). Ruzzante and Doyle (1991) stated that selection of fish for more growth tends to favor more aggressive fish. Selection pressure on growth rate is increased if the aggressiveness is heritable. However, game theory (Doyle and Tablot, 1986) has shown that selection for rapid growth favors selecting aggressive fish. On the other hand, tolerant fish may be favored in an environment with competition (Ruzzante and Doyle, 1993).

Dominance in fish has a discernable impact on their feeding activity. Adams et al. (1998) observed that feeding activity in fish is polarized with 41% of the total feed consumed by the dominant animals. Typically, aggression has been used to suppress the foraging activity of passive animals and to inhibit co-specifics from feeding, thus causing a monopolization of food resources (Chapman, 1966; Gotceitas and Goin, 1992; Dumbrack et al., 1996). In this environment, those fish not included in feeding and fighting were left unattached, compared to others in the group. Food intake and aggression are almost always positively correlated and was experimentally proven using direct observational studies by Metcalfe (1989) who confirmed that within small groups one or two fish control almost the entire food resource and dominate their companions. Symoens (1970) in his study on Salmons stated social hierarchies may consist of aggressive, dominant, subdominant, less aggressive, and subordinate fish. In addition, food may be monopolized by one or two fish or a small group in cases of greater stocking densities.

Social Dominance and Studies in Animal Breeding and Genetics

To date, there is a paucity of research concerning social dominance in animals in the field of animal breeding and genetics. The need for more research on this topic is twofold. First, competitive effects present in farm animals would penalize subordinate animals' growth and productivity. Also, genetic studies on competitive interactions would be of great help in identifying dominant animals and how they could affect others in a group setting.

Theories on competition and its impact on selection were put forward by Falconer (1981). He concluded that "Competition is an important factor in plants, often making sib correlations largely meaningless, particularly with the characters related to yield". He also stated that competition reduces the intra-class correlations between the relatives and it may be even negative. Wright (1977) demonstrated a nonlinear response for selection using competitive

effects found in trees. A theoretical framework on interacting genotypes in breeding programs was first developed by Griffing (1967, 1968a, 1968b, 1976a, 1976b). According to Griffing, associative effects and direct effects could be included in genetic models. The expected change in the mean of selection on an individual record is given by:

$$\Delta\mu = (i / \sigma_a^2)(\sigma_d^2 + (n-1)\sigma_{ad})$$

where $\Delta\mu$ is the expected change of mean of selection, σ_a^2 is the additive associative variance, σ_d^2 is the additive direct variance, n is the number of individuals in a group, and σ_{ad} is the covariance.

The negative covariance reduces the mean for selection. If there is n group size then there could be $n-1$ interacting individuals within that group.

Classical genetics assumed only direct effects in the model and neglected the interacting effects between the genotypes. Following Falconer and Griffing, if we ignore the competitive interactions, it is possible that the selection procedure might not be accurate. Muir and Schinckel (2002) and Muir (2005) expanded the genetic model assuming the associative effects in the genetic model of analysis by including genetic competitive effects in mixed models. Environmental factors for associative effects were included by Bijma and Muir (2006). The resulting model was stated as follows:

$$Y = X\beta + Z_U D + Z_A A^G + Z_A A^E + \varepsilon$$

where Y is the vector of observations, $X\beta$ is the incidence matrix of fixed effects, $Z_U D$ is the incidence matrix of the direct effects, $Z_A A^G$ is the incidence matrix of the associative effects, and $Z_A A^E$ is the environmental associative effects.

Upon estimation of the direct and associative effects, the selection index was calculated by using the following:

$$I_i = D_i + (n - 1)A_i g$$

Muir found that contributions of the associative effects were smaller in large-sized groups and estimated more precisely in smaller groups. In addition, direct effects were estimated more precisely than associative effects. Muir concluded that estimates of genetic parameters were fairly robust in relation to errors in parameters, estimates, and group size. Experimental validation using Japanese Quails showed a negative genetic correlation between direct and associative effects is moderate to largely negative and heritability estimates for the associative effects were low.

Arango et al. (2005) conducted studies on growing Gilts using the expanded genetic model with a variable number of competitors in a pen that considered the associative genetic effect as a covariable. They found that residual variance was inflated when the pen effect was excluded. Also, the convergence rate was slow and sensitive to the starting parameters and separating the dominant animals in a pen was difficult if there was a large group size.

The comparison of models including genetic competitive effects for average daily gain was conducted for selected lines of swine by Chen et al. (2006), using the model developed by Cassady and Van Vleck (2005). When the pen effect was considered to be random, the variance components were partitioned successfully compared to considering it as a fixed effect. The researchers also found that the estimates of σ_{pg}^2 increased to 30% by ignoring the competitive effects.

Cappa et al. (2006) investigated the estimation of dispersion parameters with competitive genetic effects on Pines via a Bayesian approach. They assumed a variable number of

competitors in the model and also the relationship between them. Conjugate priors were used to estimate the genetic covariance. Through the recovery of symmetric marginal posterior distributions, the researchers concluded that the highest probability density of dispersion parameters did not include 0, suggesting that the parameters did not include 0. Biased estimates in the dispersion parameters were observed by ignoring the competitive interactions and additive relationships between competitors. There was no convergence problem in estimating the parameters.

Rutten et al. (2006) applied the proposed models incorporating the competitive effects to aquaculture while researching genetic variations of competitive behavior in Nile Tilapia. Variance components that were estimated excluding the tank effects were 0 and were omitted from the model; the estimate of competitive effects was almost 0. Interactions among animals may contribute to the heritable variation among animals. Bijma (2007b) extended the Muir model and introduced the covariance structure for the residuals, $\sigma_{E_{ds}}$, which represents the non-heritable measure for competition and cooperation. Bijma found that two-thirds of the total heritable phenotypic variation in the survival rate of chickens was contributed by the interactions. Bijma (2007b) reported there is a possibility of estimating genetic parameters for underlying interaction traits, but it requires substantial information from the data. Bijma (2007b) estimated a genetic correlation between the direct and associative effects to be 0.28, indicating that animals may benefit from being passive. Interactions could also be reduced by using group selection strategy (Bijma et al., 2007a). Group selection is not used frequently in breeding as the selection of candidates in groups interfere with the regular individual recording of the data and may also increase the loss of selection of candidates by aggression and infectious diseases. Esher (2007) found that selection based on information from relatives kept in family groups enables a

fairly greater response towards selection. The main drawback with using information of relatives is the basic assumption of homogenous groups (full sibs and half sibs) which does not hold well in commercial conditions; however, with the unrelated individuals the index selection performed worse.

Recently, Misztal and Rekaya (2007) presented new models of social dominance, assuming that social dominance is expressed nonlinearly. They assumed the binary case, when only one animal per pen is dominant, to be unique. In this environment, the dominant animal could either have a fixed advantage over passive animals or that advantage could be a function of the breeding value.

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CHAPTER 3

MODELING SOCIAL COMPETITION ASSUMING A SINGLE DOMINANT ANIMAL PER PEN

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ABSTRACT

The model of social competition by Muir and Schinckel (2002) assumes a continuous expression of social dominance. The purpose of this study was to examine a model where such an expression is binary. The simulation involved 3 generations of 6,000 animals housed in pens of size 6. Two additive values, direct and social dominance, were assigned to each animal; both effects were assumed correlated. Liability to social dominance was calculated as a sum of the social dominance effect plus a residual. An animal with the greatest liability per pen was declared dominant in that pen. Growth was calculated as a sum of effects of pen, generation, direct, dominance advantage, and the residual. The effect of dominance advantage was only present in records of dominant animals and was a fixed value in model M1 or equal to the effect of social dominance plus constant in model M2. The analyses used a bivariate linear-threshold where the second trait was the dominance status assumed known. Initial analyses assumed M1. When the second trait was ignored, the estimate of the dominance advantage was unbiased when the covariance was 0, was biased upwards when the covariance was positive, and downwards if negative. There was no bias when the second trait was considered. Variance components were estimated using MCMC for a scenario with a positive correlation. There was an upward bias for the direct variance and downward for the competitive variance and the covariance. The biases were traced to one threshold used for all records. A variable threshold is required so that exactly one animal per pen is selected as dominant. Variance components were estimated and animal effects predicted with the MS model. The correlations between the competitive effects from the 2 models were close to 0. When the model was changed to M2, the same correlation was -0.1. Modeling social dominance with different models may result in drastically different rankings.

Different models are needed to account for different types of social interactions in different species.

Key words: aggression, associative effects, competition, social dominance

INTRODUCTION

Animal welfare is an important concern in animal production. One factor of particular interest in animal welfare is competition among animals penned together. Farm animals (pigs, chicken, and fish) have aggressive interactions that can decrease the productivity of the animals within a pen. In an evenly matched group, the heaviest animals tend to be the most aggressive ones, gaining the most weight. On the other hand, aggression has been correlated with social dominance but not with the weight in an unevenly matched group (Tindsley, 1984). Turner et al. (2001) suggested that domestic pigs under commercial conditions exhibit dyadic dominance relationships and the number of dyadic relationships established increases linearly with group size. Further, Hughes et al. (1997) reported that the frequency of aggressive behaviors of laying hens in stable flocks of 700 was considerably less than the ones reported for smaller group sizes.

The competitive interactions in farm animals can be addressed by including a component of competitive interactions between the pen mates in a model for genetic analysis. Muir and Schinckel (2002) included the competitive effects of pen mates along with the direct effect. Van Vleck and Cassady (2003) investigated the competitive model using a simulation study, producing unexpected results even though they could recover simulation parameters. Arango et al. (2005) concluded that estimating the variance components of competitive effects is difficult with a small amount of data and in a low competitive environment. Chen et al. (2005) concluded that when pen effect and competitive effects are included in the statistical analysis the variance due to competitive effects is small.

Recently, Misztal and Rekaya (2007) presented new models of social dominance, assuming that social dominance is expressed nonlinearly. They found the binary case, when only one animal per pen is dominant, to be unique. In this environment, the dominant animal could either have a fixed advantage over passive animals or that advantage could be a function of the breeding value. The purpose of this study was to examine a model where such an expression is binary and to compare this with the model by Muir and Schinckel (2002).

MATERIALS AND METHODS

Data Simulation

Growth was simulated using the binary model by Misztal and Rekaya (2007). Due to the computational complexity of a model with k categories, a simplified model with only two categories ($k = 2$) was used in this study, assuming a single dominant animal per pen. Consequently, the model in (Misztal et al., 2007) could be rewritten as model, M1:

$$y_{ijklm} = g_{1j} + a_{1i} + p_{1m} + f \delta(y_{2ijklm} = "1") + e_{ijklm} \quad (1)$$

where y_{ijklm} was the observed growth data of each pig (i), g_{1j} was the fixed effect of generation class j, a_{1i} was the random additive effect of each pig (i), p_{1m} was the random effect of pen class m, f was the effect of category on each pig (i), δ was the covariable of dominance advantage, and e_{ijklm} was the random residual term.

The liability to social dominance is described as:

$$l_{2ijklm} = g_{2j} + a_{2i} + p_{2m} + e_{2ijklm} \quad (2)$$

where l_{2ijklm} was the non-observed liability for each pig (i), g_{2j} was the fixed effect of generation class j, a_{2i} was the random additive associative effect of each pig (i), p_{2m} was the random effect of pen class m, and e_{2ijklm} was the random residual term.

The direct additive and competitive effects were assumed correlated as follows:

$$G = \begin{bmatrix} \sigma_d^2 & \sigma_{da} \\ \sigma_{ad} & \sigma_a^2 \end{bmatrix}$$

where σ_d^2 was the variance of the direct additive effect, σ_a^2 was the variance of the direct associative effect, and σ_{ad} was the covariance between direct additive and associative effects.

For each pen, the animal with the greatest liability, as indicated in Eq. 2, was assumed to be dominant ($y_{2ijklm} = 1$); the rest of the animals in the pen were assumed to be submissive ($y_{2ijklm} = 0$).

The model in Eq. 1 assumed that the advantage of a dominant animal was a fixed value. A refinement of the model in Eq. 1 that allows for dominance advantage to differ using the animal's associative effect can be presented as model, M2:

$$y_{ijklm} = g_j + a_{1i} + p_m + (f + a_{2i})(\delta_j = "1") + e_{ijklm} \quad (3)$$

Generating pedigree and data. One fixed effect (generation), two random effects (animal additive and pen effect), and the dominance advantage were used to generate data. Fixed effects were generated from a uniform distribution (U (-2, 2)); the random effects, animal additive, pen effects, and residual were generated from a multivariate normal distribution with a 0 mean and variance-covariance matrix structure of the following:

$$G = \begin{bmatrix} 10 & 1 \\ 1 & 1 \end{bmatrix}, R = \begin{bmatrix} 10 & 0 \\ 0 & 1 \end{bmatrix}, P = \begin{bmatrix} 10 & 0 \\ 0 & 1 \end{bmatrix}.$$

The growth phenotype (y_{1ijklm}) was calculated as the sum of the effects of the pen, generation, direct, dominance advantage, and the residual. The effect of the dominance advantage was only added to the records of dominant animals ($y_{2ijklm} = 1$). The dominant animal advantage (δ) was fixed at 10 or 3 and added to the phenotypic record of the animal for dominant

animals in model [M1]. In model [M2], the dominant advantage added to the phenotypic growth record of the animal was the breeding value of the associative effect. Each animal has one record for each trait and no records were assigned to the animals in the base population. Animals were randomly distributed to pens across generations. Three generations of pedigrees were used for all the models assuming that males were randomly mated with females and there was no selection of animals within each generation. Data and pedigree structure generated with a simulation program are presented in Table 3.1.

Statistical analysis. A univariate analysis of the linear (y_{1ijklm}) model, M1 excluding the binary trait (y_{2ijklm}) was done to investigate the biases for the added dominance advantage. The model, M1 was further analyzed as a two-trait model, with y_{1ijklm} as the linear trait and y_{2ijklm} as the binary trait, using the linear-threshold program. Variance components and the dominance advantage were assumed to be known. The bivariate analysis was run with different sets of variance and covariance structures of pen, animal additive, and residual variance. The structures of those models used in the analysis are presented in Table 3.2. In a scenario with a negligible bias in the dominance advantage (δ) estimation, variance components were estimated using MCMC simulations via a Bayesian approach.

Comparison with the Muir model. Muir (2005) proposed an expanded genetic model having direct and associative effects:

$$y_{ijklm} = g_k + p_l + a_i + \sum c_j + e_{ijklm} \quad (4)$$

where y_{ijklm} was the observed weight of each pig (i), g_k was the fixed effect of generation class k , p_l was the random effect of pen class l , a_i was the direct additive genetic effect of each animal i , c was the competition or associative additive genetic effects summed over the j pen mates of animal i , and e_{ijklm} was the random residual term.

Univariate analysis of Muir's model was carried out with a variance and covariance structure for the direct additive and competitive effects. Correlations were computed between the true breeding values and the predicted breeding values for the direct and competitive animal effects. Variance components were estimated using MCMC simulations via a Bayesian approach. Correlations between the true (simulated) and predicted breeding values for the direct and competitive animal effects were computed using model's M2 and Muir's. All analyses were replicated ten times.

RESULTS AND DISCUSSION

Results of the univariate analysis for the continuous trait in model, M1 with the dominance advantage but excluding the binary data (y_{2ijklm}) are presented in Table 3.3. The estimated dominance advantage had a lowest bias with a combination of extremely low residual (0.001) and direct additive variance (0.001). Greatest biases are observed when there was realistic residual (8) and pen variance (8).

Table 3.4 shows the bivariate analysis of the model, M1 as a continuous trait with a dominance advantage and y_{2ijklm} as binary data. Biases with a dominance advantage are the greatest when the pen variance was greater. Biases are almost 0 in a specific combination of low additive and pen variance and 0 (co) variance for pen effect between two traits. Greatest biases were recorded when not only pen but also the residuals are correlated and the pen variance was high.

Table 3.5 shows estimates of the dominance advantage with the model using pen as a random or a fixed effect. The biases were low (3.02 to 3.14 compared to 3) with the model treating pens as a fixed effect to random effect.

Table's 3.6 and 3.7 show estimates of the dominance advantage for different variance components for direct, associative, and pen effects. The results show that the estimated dominance advantage was almost similar to the true value when the additive covariance was -1 or +1 and the pen effect was excluded from the binary trait. Biases are high when the additive covariance was excluded from the analysis and the pen variance was included, as seen in Table 3.7. When the second trait was ignored, the estimate of the dominance advantage was unbiased when the covariance was 0, biased upwards when the covariance was positive, and downwards if negative. There was no bias when the second trait was considered in the analysis.

Variance components were estimated using a Bayesian approach via MCMC for a scenario with a positive correlation. There was an upward bias for the direct variance and downward for the competitive variance and the covariance. These biases were traced in part to the fixed threshold used in the analyses. The estimated variance components for that dataset are shown in Table 3.8. They are in close agreement with values used in the simulation. Estimates of the direct additive variance, associative variance, pen variance, and residual variance were 10.15, 0.86, 9.80, and 9.92, respectively. The convergence was fast (Figure 3.1).

Comparison with the Muir Model

Table 3.9 shows variance components estimated with Muir's model. Most of the estimated variances are almost similar to those that were simulated. However, the variance of the genetic associative effect was very small. Estimates of direct additive, associative, pen, and residual variance's were 9.87, 0.02, 9.70, and 11.08, respectively. The correlations for the direct genetic effect between the predicted and simulated breeding values were fair (0.6) but the correlations between the associative effects were almost 0.

Table 3.10 shows correlations between the predicted breeding values and simulated for Muir's model and comparison between model M2 and Muir's model. The correlations are 0.55 and 0.72 for the direct effect between the real and predicted breeding values for models M2 and Muir's model, respectively. The correlations are 0.30 and -0.07 for the associative effect between the real and predicted breeding values for model, M2 and Muir's model, respectively. The correlation shows that for the model, M2 the correlations for the associative effect are almost 0. Different models may be needed to account for different types of social interactions in different species.

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Table 3.1 Summary description of the simulated data

Total Number of Animals	18500
Base Population	500
Number of generations	3
Number of pens	3000
Number of animals in pen	6
Number of dominant animals per pen	1
Sex ratio(M:F)	1:5
Heritability for the additive effect	33%
Heritability for the associative effect	50%

Table 3.2 Different models used in the analysis with model, M1

MODEL ¹	GEN	PEN	ADDITIVE	COVARIABLE	RESIDUAL
1	RANDOM*	RANDOM	RANDOM	RANDOM	RANDOM
2	RANDOM	FIXED	RANDOM	RANDOM	RANDOM
3	RANDOM	RANDOM	RANDOM	RANDOM	RANDOM

RANDOM*: Used as random effect; FIXED: used as fixed effect in analysis.

Table 3.3 Estimates of dominance advantage (δ) for various values of variances in model (M1) with the second trait excluded

$\Sigma_e^{2 \ 1}$	σ_g^2	σ_p^2	Dominance advantage
3	2	1	11.6
2	1	1	11
3	1	3	11.04
2	1	2	11.03
3	1	3	11.04
4	1	5	11.6
6	1	3	11.35
7	1	2	11.34
1	1	2	11.35
-	1	2	10.44
-	1	-	10.5
-	-	2	10.01
2	1	-	10.92
8	1	-	13.22
8	2	-	13.1
8	2	8	13.07

σ_g^2 : Direct additive variance, σ_p^2 : Pen variance, $\sigma_e^{2 \ 1}$ Residual variance, dominance advantage (true value=10)

Table 3.4 Estimates of dominance advantage (δ) for variance parameters of linear-threshold model (M1)

Σ_d^2	σ_a^2	σ_{ad}	σ_{e1}^2	σ_{e2}^2	σ_{e1e2}	σ_{p1}^2	σ_{p2}^2	σ_{p1p2}	Dominance advantage (δ)
10	10	0	1	1	0	0.01	0.01	0	10.22
10	10	5	1	1	0.5	10	10	0.5	11.59
10	10	5	1	1	0.5	5	5	2.5	10.39
10	10	5	10	1	0.1	5	5	2.5	10.36
10	10	5	20	1	0.5	5	5	2.5	10.62
10	10	5	20	1	0.5	5	5	2.5	10.49
10	10	0	20	1	0	5	5	0	9.57
10	10	0	20	1	0	5	5	0	11.06
-	-	0	1	1	0	-	-	0	11.04
									11.48
-	-	0	1	1	0	-	-	0	10.03

σ_d^2 : direct additive variance, σ_a^2 : associative variance, σ_{p1}^2 : pen variance for direct additive effect, σ_{p2}^2 : pen variance for associative additive effect, σ_{e1}^2 : residual variance for direct effect, σ_{e2}^2 : residual variance for associative effect, σ_{ad} : (co)variance between direct and associative effects, σ_{e1e2} : (co) variance between direct and associative effects for residual, σ_{p1p2} : (co) variance between direct and associative effects for pen effect, dominance advantage (true value=10).

Table 3.5 Estimates of the dominance advantage (δ) with pen as fixed/random effect for different set of variances with model M1

Σ_d^2	σ_a^2	σ_{ad}	σ_{e1}^2	σ_{e2}^2	σ_{e1e2}	σ_{p1}^2	σ_{p2}^2	σ_{p1p2}	Simulated Dominance advantage	Rep1	Rep2	Rep3
10	1	0	10	1	0	10	1	0	3			
10	1	0	10	1	0	10	1	0	3	3.14	3.09	3.02
10	1	0	10	1	0	10	1	0	3			
10	1	0	10	1	0	0	0	0	3	2.99	3.04	3.0

σ_d^2 : direct additive variance, σ_a^2 : associative variance, σ_{p1}^2 : pen variance for direct additive effect, σ_{p2}^2 : pen variance for associative additive effect, σ_{e1}^2 : residual variance for direct effect, σ_{e2}^2 : residual variance for associative effect, σ_{ad} : (co)variance between direct and associative effects, σ_{e1e2} : (co) variance between direct and associative effects for residual, σ_{p1p2} : (co) variance between direct and associative effects for pen effect, Rep1, 2, 3: estimated social dominance advantage for three replicates.

Table 3.6 Estimates of the dominance advantage (δ) with positive/negative additive covariance for associative effect with model M1

σ_d^2	σ_a^2	σ_{ad}	σ_{e1}^2	σ_{e2}^2	σ_{e1e2}	σ_{p1}^2	σ_{p2}^2	σ_{p1p2}	Simulated Dominance advantage	Rep1	Rep2	Rep3
10	1	-1	10	1	0	10	1	0	3			
10	1	-1	10	1	0	10	1	0	3	3.10	3.01	3.13
10	1	1	10	1	0	10	1	0	3			
10	1	1	10	1	0	10	1	0	3	3.05	3.20	2.99

σ_d^2 : direct additive variance, σ_a^2 : associative variance, σ_{p1}^2 : pen variance for direct additive effect, σ_{p2}^2 : pen variance for associative additive effect, σ_{e1}^2 : residual variance for direct effect, σ_{e2}^2 : residual variance for associative effect, σ_{ad} : (co)variance between direct and associative effects, σ_{e1e2} : (co) variance between direct and associative effects for residual, σ_{p1p2} : (co) variance between direct and associative effects for pen effect, Rep1, 2, 3: estimated social dominance advantage for three replicates.

Table 3.7 Estimates of the dominance advantage (δ) excluding associative effect and including pen effect with model M1

σ_d^2	σ_a^2	σ_{ad}	σ_{e1}^2	σ_{e2}^2	σ_{e1e2}	σ_{p1}^2	σ_{p2}^2	σ_{p1p2}	Simulated Dominance advantage	Rep1	Rep2	Rep3
10	1	1	10	1	0	10	1	0	3			
10	1	0	10	1	0	10	1	0	3	3.93	3.63	3.67
10	1	-1	10	1	0	10	1	0	3			
10	1	0	10	1	0	10	1	0	3	2.37	2.27	2.40

σ_d^2 : direct additive variance, σ_a^2 : associative variance, σ_{p1}^2 : pen variance for direct additive effect, σ_{p2}^2 : pen variance for associative additive effect, σ_{e1}^2 : residual variance for direct effect, σ_{e2}^2 : residual variance for associative effect, σ_{ad} : (co)variance between direct and associative effects, σ_{e1e2} : (co) variance between direct and associative effects for residual, σ_{p1p2} : (co) variance between direct and associative effects for pen effect, Rep1, 2, 3: estimated dominance advantage for three replicates.

Table 3.8 Variance components estimation with linear-threshold model (M1)

	σ_d^2	σ_a^2	σ_{ad}	σ_{e1}^2	σ_{e2}^2	σ_{e1e2}	σ_{p1}^2	σ_{p2}^2
Simulated	10	1	1	10	1	0	10	0
Estimated	10.15	0.86	0.93	9.98	1.07	0	9.92	0

σ_d^2 : direct additive variance, σ_a^2 : associative variance, σ_{p1}^2 : pen variance for direct additive effect, σ_{p2}^2 : pen variance for associative additive effect, σ_{e1}^2 : residual variance for direct effect, σ_{e2}^2 : residual variance for associative effect, σ_{ad} : (co)variance between direct and associative effects, σ_{e1e2} : (co) variance between direct and associative effects for residual.

Table 3.9 Variance components estimation with Muir's model

	$\sigma_d^{2\ 1}$	σ_a^2	σ_{ad}	σ_p^2	σ_e^2
Simulated	10	-1	1	10	10
Estimated	9.87	0.02	0.13	9.70	11.06
Simulated	10	-2	1	10	10
Estimated	7.88	0.18	0.13	9.99	11.18
Simulated	10	-3	1	10	10
Estimated	7.19	-0.23	0.07	10.17	11.13

$\sigma_d^{2\ 1}$: direct additive variance, σ_a^2 : associative variance, σ_p^2 : pen variance, σ_e^2 : residual variance, σ_{ad} : (co)variance between direct and associative effects.

Table 3.10 Correlations between the predicted and simulated breeding values for model M2 and Muir's model

	a ¹	b	c	d	k1	k2
a	1	0.28	0.73	-0.50	0.55	-0.30
b	0.28	1	0.14	-0.10	0.12	-0.07
c	0.73	0.14	1	-0.75	0.72	-0.38
d	-0.50	-0.10	-0.75	1	-0.49	0.28
k1	0.55	0.12	0.72	-0.49	1	-0.63
k2	-0.30	-0.07	-0.38	0.28	-0.63	1

a¹=predicted breeding value for additive effect with model 3, b=predicted breeding value for associative effect with model 3, c=predicted breeding value for additive effect with model 4, d=predicted breeding value for associative effect with model 4, k1=simulated breeding value for additive effect, k2=simulated breeding value for associative effect.

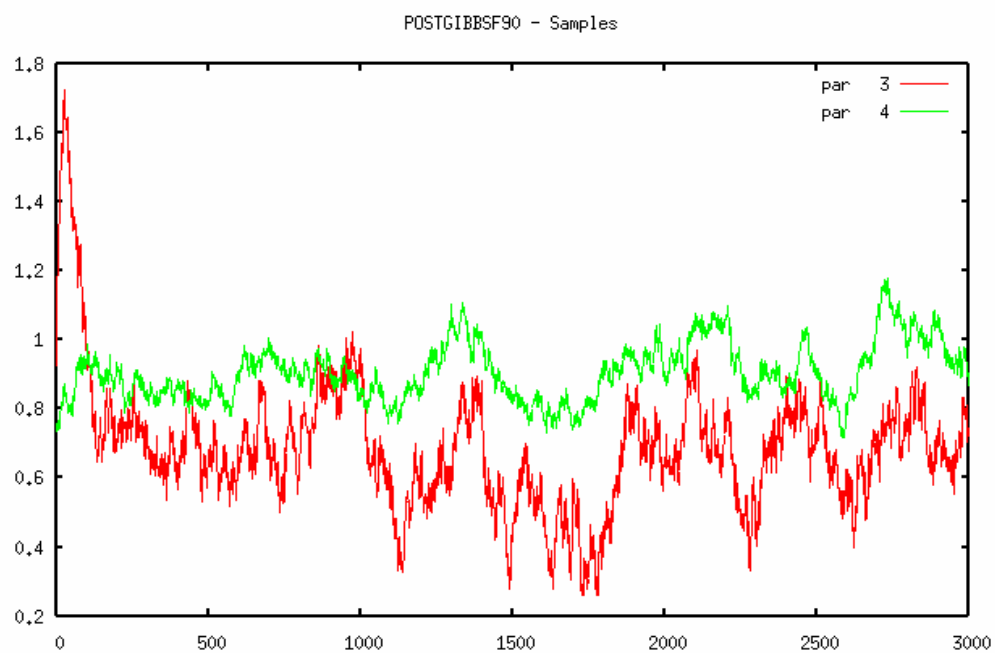


Figure 3.1 Samples of genetic parameters obtained from the Gibbs sampler

CHAPTER 4

**BAYESIAN IMPLEMENTATION TO PREDICT THE DOMINANT STATUS OF
ANIMALS USING GROWTH DATA**

¹ J. M. Achi, R. Rekaya and I. Misztal. To be submitted to *Journal of Animal Science*.

ABSTRACT

A simulation study was conducted in order to predict the dominance status of penned pigs based on their growth data using a Bayesian procedure. The body weight of pigs at 18 wk of age was used as an indirect predictor of the dominance status. Data was simulated to mimic body weight using a mixed linear model that included generation and a covariate for the social dominance as fixed effects and pen, animal as random effects. The data file consisted of body weight on 5400 animals generated in 900 pens (6 pigs per pen) assuming only 1 dominant animal per pen. Social dominance was set to minus one -1 for non-dominant pigs and ranged from 0.5 to 2 residual standard deviations for dominant animals. A Bayesian approach via Gibbs sampling was used to predict the animal's dominant status and to infer all the model parameters. The probability of identifying the true dominant animal in each pen was 0.31, 0.52, 0.75 and 0.85 when the dominance effect was 0.5, 1, 1.5 and 2 residual standard deviations, respectively. Therefore, the proposed procedure has increased the probability of identifying the true dominant animal by 200 to 600%, compared to random assignment. When the dominance effect was smaller or equal to one residual standard deviation, the bias in the estimation of the genetic, pen, and residual variances was low to moderate. However, for higher social dominance effect (more than one residual standard deviation) the bias in all variance components is substantial. These results are expected due to the fact that every miss-identification of the true dominant animal will dramatically increase the residual terms in the model and consequently the over estimation of the residual variance and a reduction of the genetic and pen variances. Based on the results of this simulation study, it is evident that a high identification probability of the true dominant animals can be achieved. However, that could be associated with a high price expressed by a severe bias in the estimation of the variance components. Consequently, it is recommended to strike a

balance between identification and bias. Furthermore, it is important to evaluate the performance of the proposed procedure in real commercial set up and to compare it to currently used methods.

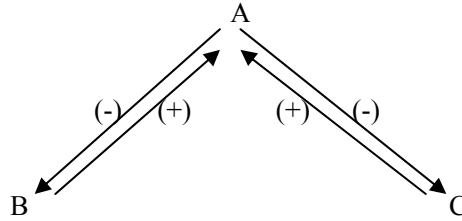
Key words: Social dominance, Simulation, Bayesian

INTRODUCTION

Several production traits are affected by the dominance status of animals in the same environment. Social dominance exhibited by animals in an organized hierarchy is assumed to be a quality naturally possessed by an animal in its own way (Powell, 1974) and is exhibited in varying degrees. In an evenly matched group of animals, the heaviest ones tend to be the most aggressive and generally gain more weight. However, in an unevenly matched group of animals, aggression is often correlated with social dominance and not necessarily with body weight (Tindsley, 1984).

In the last decade, competition and aggressiveness between farm animals has become an area of active research not only due to its importance in livestock productivity but also for its animal welfare advantage. Muir & Schinckel (2002) and Muir (2005), expanded the classical genetic evaluation model through the inclusion of associative effects in order to account for the competition between penned animals. Over the years, several variations of this model have been proposed and applied to different livestock species (Arango et al., 2005; Van Vleck and Cassady, 2005; Chen et al., 2006; Cappa et al., 2006). More recently, Misztal and Rekaya (2007) presented a nonlinear model to account for social dominance. In their special binary case, only one animal per pen was assumed dominant with a fixed or varying (function of the breeding value) advantage over passive animals. An alternative approach is to have an advantage for dominant animals and a penalty for the passive ones. This principle could be summarized in the following simplified diagram. In a pen with three animals (A, B, and C) where animal A is

assumed dominant, the latter will receive a positive social dominance advantage (**SD**), indicated by the plus sign in the figure, and it penalizes B and C with the same amount of SD (indicated by the negative signs).



Positive and negative effects of social dominance between three penned animals

The main objective of this study was to evaluate the possibility of predicting the dominance status of jointly penned animals under varying magnitudes for social dominance effects based on growth data.

MATERIALS AND METHODS

Data simulation

A simplified mixed linear model was used to simulate a data set that mimics body weight at 18 wk of age in pigs. The model included the fixed effects of generation and social dominance (as a covariate) and random effects of animal, pen, and residual terms. Statistically, the growth trait was as follows:

$$y_{ijkl} = \mu + g_j + a_i + pe_k + sd_k(\gamma) + e_{ijkl} \quad (1)$$

where y_{ijkl} is the 18th week body weight of pig i in generation j and pen k ; a_i is the direct additive effect; sd is the social dominance advantage; γ is an indicator variable that takes the value of 1 (for dominant animals) or -1 (for passive animals); and e_{ijkl} is the residual term. Social dominance advantage was set equal to 0.5, 1, 1.5, and 2 residual standard deviations. The fixed effect of generation was drawn from a uniform distribution $U [-4, 4]$. The pen and animal effects were

generated from $N(0,10)$ and $N(\mathbf{0}, \mathbf{A}\sigma_a^2)$, respectively. The genetic variance and the overall mean, μ , were set equal to 20 kg² and 84 kg, respectively. The residual terms were sampled from a normal distribution with mean 0 and variance equal to 34 kg². The phenotypic growth record of each animal was calculated by adding the effects of all factors in the model. The pedigree included a base population of 500 animals and three subsequent generations of 1800 animals. Mating as well as allocation of animals to pens was random. A summary description of the data and pedigree structures could be found in Table 4.1. Values of social dominance used in different simulation scenarios are presented in Table 4.2.

Statistical analysis

A Bayesian approach via MCMC simulations was used to predict the status of the dominant animals. Assuming a flat prior for dominance status assignment for each animal in a particular pen, k , the posterior probability of an animal i being dominant (p_{ki}) is given by:

$$p_{ki} = p(\mathbf{y}_k | \beta, pe_k, \mathbf{u}, i = dom) / \sum_{j=1}^6 p(y_k | \beta, pe_k, \mathbf{u}, j = dom)$$

where $p(\mathbf{y}_k | \beta, \mathbf{u}, i = dom)$ is the conditional distribution of the data in pen k given that animal i was assumed dominant, $\mathbf{y}_k$, is the vector of body weights of animals in pen k , β is the vector of fixed effects, pe_k is the effect of pen k , and $\mathbf{u}$ is the vector of additive effects. The sum is over all the animals in a given pen.

Given the vector of probabilities for pen k , $\mathbf{p}_k$, the dominant animal in the pen was determined by sampling from a multinomial distribution with parameters $\mathbf{p}_k$ and $n=6$.

Once the dominant animals are identified, the implementation of the mixed model in Eq. 1 is straightforward. Using the following priors for the model parameters, the fully conditional distributions were all in closed form as follows:

$$p(\boldsymbol{\beta}) \sim U[\boldsymbol{\beta}_{\min}, \boldsymbol{\beta}_{\max}]$$

$$p(\mathbf{u} | \sigma_a^2) \sim N(\mathbf{0}, \mathbf{A}\sigma_a^2)$$

$$p(\mathbf{pe} | \sigma_p^2) \sim N(\mathbf{0}, \mathbf{I}\sigma_p^2)$$

$$p(\mathbf{e} | \sigma_e^2) \sim N(\mathbf{0}, \mathbf{I}\sigma_e^2)$$

$$P(\sigma_a^2) \sim (\sigma_a^2)^{-(\nu_a+2)/2} \exp(-1/2\nu_a s_a / \sigma_a^2)$$

$$P(\sigma_p^2) \sim (\sigma_p^2)^{-(\nu_p+2)/2} \exp(-1/2\nu_p s_p / \sigma_p^2)$$

$$P(\sigma_e^2) \sim (\sigma_e^2)^{-(\nu_e+2)/2} \exp(-1/2\nu_e s_e / \sigma_e^2)$$

where the ν_i and s_i^2 ($i = a, p, e$) are the a priori degrees of freedom and scaling factors for the three variance components. In this study, ν_i was set equal to 5, while s_i^2 was equal to the true value of the variance component i .

In fact, for position parameters (fixed and random effects) their conditional distributions were normal with known means and variances. The conditional distributions for the three variance components (pen, animal, and residual variances) were scaled inverted Chi square with known scaling factor and degrees of freedom.

In all scenarios, a unique chain of 10,000 iterations was implemented. The required burn-in period was 1,000 rounds. The remaining 9,000 iterations were retained without thinning for post Gibbs analysis. Every simulation scenario was replicated 5 times and the reported results are based on their average.

To summarize, the proposed procedure was implemented using the following steps:

1. Dominant animals were randomly assigned in each pen.
2. $\boldsymbol{\beta}, \mathbf{u}, \mathbf{pe}, \mathbf{sd}$ were sampled from their respective conditional distribution given the current assignment of dominant animals.

3. $\sigma_a^2, \sigma_p^2, \sigma_e^2$ were drawn from their respective conditional distributions.
4. The probability of social dominance was calculated for each animal in every pen.
5. The assignment of the dominant animal in each pen was done through sampling from a multinomial distribution.
6. An update of the dominant status was determined.
7. Steps 2 to 6 were repeated until convergence.

In each round of the sampling process, the dominance status of every animal in the data was computed. At the end of the sampling process, the probability of each animal being dominant was computed as:

$$pd_{ik} = \frac{\text{number of times animal } i \text{ was identified as dominant in pen } k}{\text{total number of iterations}}$$

RESULTS AND DISCUSSION

Table 4.2 presents the average probabilities (over five replicates) for identifying the true dominant animals with varying magnitude of the social dominance effect. As expected, the predicted probabilities increased with the increase in the magnitude of the social dominance advantage. This is due to the fact that large social dominance effect makes body weight differences between animals in the same pen exceed what is expected by random chance. In fact, when social dominance was half of the residual standard deviation, the predicted probability was 31% or twice what would be achieved randomly (16%). Such probability was increased to 52, 75, and 85% when the social dominance effect was 1, 1.5, and 2 residual standard deviations, respectively. Furthermore, the increase in identification probabilities is almost linear, as depicted in Figure 4.1. The results observed in this study tend to agree with what has been reported in the literature. In fact, Andersson (1994) reported, in a study of the relationship between weight asymmetry and aggression in pigs from different environments, that larger pigs increase their

chances of winning a confrontation with smaller animals. Furthermore, he concluded that there should be at least 3 kg of weight difference between opponents to succeed in a confrontation. Aggressive interactions among animals in a pen affect growth and body weight either by penalizing the passive ones or benefiting dominant individuals by more access to feed, water, and other resources. Thus, body weight is the best indicator of resource holding potential and its variation reflects the social dominance in a group of animals. It is important to note that the three kilograms mentioned by Andersson (1994) is almost identical to the half residual standard deviation used in our study (2.91 kg).

The high probabilities (85%) obtained with very large social dominance effects further support the aggressive interactions between penned animals which will consequently affect the growth of dominant animals and their pen mates. Alternatively, in a more homogenous population with similar body weights and where the competitive environment did not favor agonistic and antagonistic behavior, the prediction of dominant animals was more difficult. However, it is relevant to mention that a high prediction probability in the presence of large social dominance effects is very unlikely to be observed in field data. On the other hand, identification of aggressive animals in the presence of small social dominance effects could be quite unimportant in commercial operations because it is of little interest to identify an animal which has little influence on the growth of others.

Variance components

A summary of the posterior distributions of variance components with varying levels of social dominance advantage is presented in Table 4.3. In all cases, point estimates indicate an underestimation of the additive and pen variances and an overestimation of the residual variance. Furthermore, the bias in all variance components increases almost linearly with the increase of

the social dominance effect. In fact, the bias was well over 50% for the three variance components when the social dominance advantage was twice the residual standard deviation. More alarming is the fact that in the majority of the cases the true value of the variance component is outside the high probability density interval (HPD 95%). When social dominance advantage was set to half of the residual standard deviation, the bias was minimum for pen and residual variances and their true values were well within their respective HPD 95% intervals. However, the point estimate of the genetic variance was biased (14.0 vs. 20). Although the probability of identifying the true dominant animals has increased substantially with the increase of the social dominance advantage, bias has increased at a similar rate. This could be explained by the fact that large social dominance effect makes body weight differences between animals in the same pen exceed what is expected by random chance, but at the same time any miss-identification of the true dominant animal will result in excessively larger residual terms for all animals in the pen. As a consequence, the residual variance will be biased upward and the remaining variance components will be underestimated.

Implications

Based on the results of this simulation study it seems reasonable to assume that if social dominance could induce variation in growth and body weight for jointly penned animals, the proposed methodology will be able to identify, with relatively high probability, the dominant animals. However, the proposed methodology as described in this study could lead to substantial bias in the estimation of the variance components which could have a negative impact on the selection process. It is clear that already existing methodologies such as the one for dealing with potential miss-identification of dominant animals could help alleviate the bias in the variance

components. Furthermore, it is important to evaluate the performance of the proposed method using commercial data and varying the number of dominant animals per pen.

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Table 4.1 Summary description of the simulated data

Number of animals in pedigree	5400
Base population	500
Additive variance	20
Pen Variance	10
Residual variance	34
Total number of pens	900
Number of animals per pen	6
Number of animals assumed dominant/pen	1
Heritability assumed	0.31

Table 4.2 Probability of identifying the true dominant animals using different levels of social dominance (average over 5 replicates)

Social dominance advantage	Dominant	Non-dominant
0.5*	31	69
1.0	52	48
1.5	75	25
2.0	85	15

**Values indicate the added social dominance advantage as fraction of the residual standard deviation

Table 4.3 Posterior means and standard deviation of the genetic, pen, and residual variances using different levels of social dominance (average over 5 replicates)

Social dominance advantage	Parameter	Mean	Standard deviation
0.5*	σ_d^2	14.0	1.6
	σ_p^2	10.2	1.0
	σ_e^2	40.6	1.8
1.0	σ_d^2	11.3	1.6
	σ_p^2	8.9	1.1
	σ_e^2	59.8	2.2
1.5	σ_d^2	11.3	1.9
	σ_p^2	4.9	1.0
	σ_e^2	86.8	3.0
2.0	σ_d^2	9.7	2.3
	σ_p^2	4.1	1.0
	σ_e^2	111.6	3.7

**Values indicate the added social dominance advantage as fraction of the residual standard deviation. σ_d^2 = Direct additive variance, σ_p^2 = Pen variance, σ_e^2 = Residual variance.

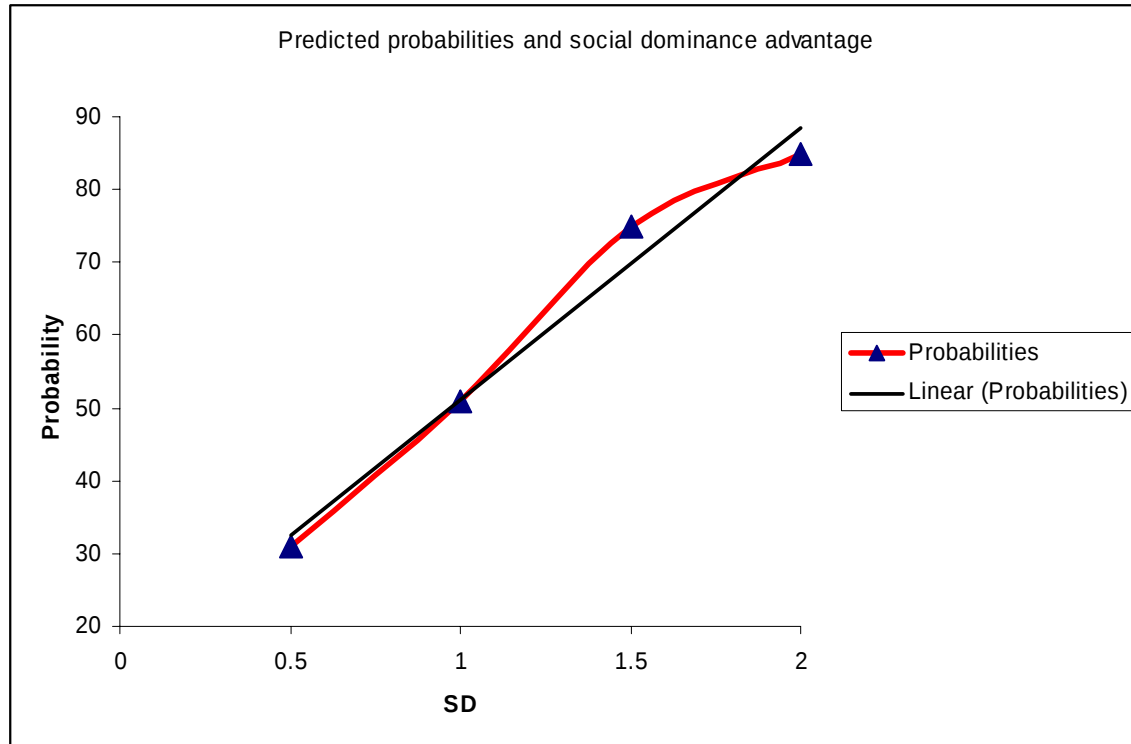


Figure 4.1 Plot of predicted probabilities and social dominance advantage

CHAPTER 5

CONCLUSION

Social dominance and aggressiveness among jointly penned animals is becoming ever more important in modern animal agriculture from productivity, consumer perception, and animal welfare perspectives. In this study, a new procedure was developed in order to account for social dominance within models used for genetic evaluation. The binary approach presented in the first paper of this study presents a different and innovate way for modeling the recursive relationship between growth and social dominance status. In order to address the major drawback of the first paper, which was the assumption of the complete knowledge of the social dominant status of every animal in each pen, we developed a Bayesian procedure capable of identifying, with reasonable accuracy, the missing dominant status. This study was based on simplified simulation scenarios seldom to be found in a commercial setup. Therefore, it is imperative to extend the proposed methods to real production system conditions in order for them to have any practical interest. This will require the consideration of a variable number of dominant individuals within a pen, reducing the bias in the estimation of variance components and the integration of genetic and social dominance factors.