Slovak J. Anim. Sci., 41, 2008 (4): 166 - 172

Review article

GENETICS OF BEHAVIOUR IN CATTLE

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ABSTRACT

Behavioural genetics is an important area of research, because the behavioural repertoire of domestic animals is so rich and complex, with striking similarities and differences between species and all of its effects on animal welfare and productivity. This review is directed on the genetics of behaviour, we explain how behavioural genetics can be used in breeding programmes and to learn more about the genetic variation in these traits. It includes examples from dairy cattle as well as beef cattle and illustrates the need for comparative studies. We provide an overview of studies on cattle that emphasises an inter-individual variability and a relative intra-individual consistency in fear responsiveness and discuss problems that may hinder the genetic evaluation and the application of temperament traits for genetic selection.

Key words: cattle, genetics, handling, fearfulness, temperament, social behaviour, maternal behaviour

INTRODUCTION

Selection for production is associated with negative behavioural effects. The genetic changes that occurred during domestication were a result of selection pressures, as well as random processes (inbreeding and genetic drift). Concern about animal welfare has led to greater use of production systems in which animals are kept in groups, and in such systems social behaviour can have an impact on production and health. Moreover, in modern animal production, where supervision is kept to a minimum, animals are required to behave well. Animals have adapted their behaviour during domestication and we need to investigate the genetics of domestication to understand why they behave the way they do. The current changes in husbandry systems, such as a general reduction of labour or an increase in herd size, incur a general reduction in human time spent caring for the animals. It reduces the opportunities for animals to become familiar with humans and increases their opportunities to perceive handling as stressful.

The genetics of behaviour involves genetic analysis of behavioural phenotypes. The genetic background, the environment and the interaction of heredity and environment result in the phenotypic expression of a behaviour. However, behaviour of cattle is difficult to measure, measures are of long duration and therefore it is difficult to obtain enough data for genetic analysis. Another source of problems is when qualitative parameters, rarely displayed traits or behavioural disturbances, which show only a few animals in the observed group, are analysed.

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Received: May 19, 2008; Accepted: September 9, 2008

ISSN 1335-3686

Handling

Cattle show individual variation in their behavioural responses to handling and management systems on farms. These behavioural responses are presumed to reflect underlying temperament traits such as fear or aggression. The level of cattle reactivity is related to human and cattle safety and welfare, herd productivity and meat quality (Fordyce et al., 1988; Grandin, 1993). For a long time, the domestication process has changed not only the animals' physical characteristics but also behavioural characteristics towards those suited to human requirements, such as social grouping tendencies, short flight distance to humans and adaptability to a wide range of environmental conditions (Price, 1984). Result of growing dairy and beef cattle husbandry throughout Europe is that contact between human and an individual animal becomes increasingly limited. Most contact is restricted to neutral or averse situations for the animal, requiring catching, fixation and treatment. Handling problems cause higher labour costs, injuries to stockpersons and cattle or even deadly accidents. Therefore, farmers are demanding docile cattle with "good temperament", which enable easy, safe and fast handling. Heritability for movement of weaners during isolation in a scale is estimated at 0.36 (Prinzenberg et al., 2006). Gauly et al. (2001) indicated that German Angus cattle are easier to handle when compared with German Simmental. When approachability was measured by the distance between a human observer and the cow when the cow first showed avoidance behaviour, dairy breeds were more approachable than beef breeds (Hohenboken, 1986). A few studies have reported a significant sex effect on temperament traits, with females always more excitable or difficult to handle (Voisinet et al., 1997a; Lanier et al., 2000; Sapa et al., 2006). Reactions to human handling are generally higher in Angus cattle than in Hereford and Simmental cattle have been described as being more difficult to handle than Angus (Gauly et al., 2001).

Selection for favourable behavioural phenotypes would increase the ability of animals to cope with stressors encountered in modern agricultural systems, improving animal welfare and productivity, and human safety when handling stock. Hence information about the genetic loci that influence temperament may be of use in selective breeding programmes to select for animals with temperaments better suited to their environment.

Fearfulness

Genetic factors can also greatly reduce or increase fear reaction in domestic animals. In the last years, the selection and quantitative genetics have improved greatly the efficiency of selection of cattle. Single-minded selection for production traits resulted in cattle with more excitable temperaments (Grandin, 1994). Recent research has shown that cattle with an excitable temperament have lower weight gains and more meat quality problems (Voisinet et al., 1997a,b). The selection away from a very excitable temperament would be beneficial. However, overselection for an excessively calm temperament could possibly result in some unknown detrimental trait (Grandin and Deesing, 1998; Maffei et al., 2006).

In addition, defensive reactions against humans are still observed in cattle even though reduced fear of humans is generally considered to be a major component of domestication (Boissy, 1995). In relation to the evolutionary history of the species, fear may also be elicited by specific stimuli, such as height and darkness. In addition, an event can elicit fear by being associated by previous experience to another alarming event. The fear-eliciting nature may be first due to its novelty. It can also be related to some physical characteristics of its presentation, such as movement, intensity, duration, suddenness or proximity (Bouissou et al., 2001; Fisher and Matthews, 2001). Social signals can also spontaneously elicit fear, such as the odour of urine collected from stressed conspecifics that induce fear-related responses in heifers (Boissy et al., 1997). The expression of fearfulness is the result of interactive processes related to past experiences and the animal's genetic background (Boissy, 1998).

Large differences in fear responses have been observed between breeds in the novel arena test (Le Neindre, 1989). Genetic influences on fear are also clearly shown in studies of sire effects. In dairy cattle, sire has a significant effect on the reactivity of cows in the milking parlour (Dickson et al., 1970). The reactions to humans are less variable between cows from the same sire than between cows from different sires (Le Neindre et al., 1996). The heritability for fear of humans explained the flight speed of 0.35 and agitation score of 0.30 (Burrow and Corbet, 2000). The estimated heritability can also change with age; the heritability of flight speed was 0.54 at 6 months and only 0.26 at 18 months of age (Burrow et al., 1988).

Some breed differences can change as a result of a particular experience. For example, cattle with Brahman genetics are generally considered to be more reactive to humans when compared with British breeds, such as Angus and Hereford (Boissy et al., 2002). However, cattle gently handled early in life are extremely docile. Therefore, the heritability of fear of humans can be low and selection may be inefficient for producing animals better adapted to human handling, particularly in a less intensive environment.

Most progress on identifying quantitative trait loci (QTL) for fear has been made with laboratory animals. Such QTL approaches have been recently extended to cattle, especially for reactions to human. Schmutz et al. (2001) determined seven QTL in calves tested for reactions to humans - one QTL was localised on each of chromosomes 1, 5, 9, 11, 15, and two QTL on chromosome 14. Fisher et al. (2001) detected several genetic markers linked with behavioural and physiological responses to humans in Limousin–Jersey crossbred cattle. From 253 microsatellite marker loci distributed on the 29 bovine autosomes, several QTL were detected for flight distance (five QTL), for plasma cortisol response (one QTL) and for urine cortisol response (two QTL). The development of marker-assisted selection could be useful for genetically influenced behavioural traits, which are not easy to measure directly in the animal. So far, QTL for fear of humans have been identified using linked markers in cattle (Boissy et al., 2002)

Consequently, the approaches to identify individual genes or markers for these genes known to quantitatively influence fearfulness traits have great promise in ruminant livestock selection to increase the ability of animals to cope with stressors encountered on farms. However, it is important to realise that there are many genes of small effect that exert influence on such behavioural traits (Boissy, 1995).

In dairy cattle, estimates for the heritability of the reactions to humans are high (0.45 to 0.53) (Sato, 1984; Dickson et al., 1970). However, other studies report low or moderate estimates, between 0.09 and 0.12 or between 0.22 and 0.25 (Visscher and Goddart, 1995). In beef cattle, a moderate heritability of 0.22 was estimated for reactions to handling (Le Neindre et al., 1995).

Temperament

Temperament can be defined as the behavioural response of the animals to handling by humans. Cattle temperament is heritable, being described as a trait of moderate heritability, partially determined by an individual animal‘s fear response (Le Neindre et al., 1995; Fordyce et al., 1996; Davis and Denise, 1998; Murphey et al., 1980; Boissy and Bouissou, 1995) and may be considered in selection programmes, searching for less excitable animals. Dickson et al. (1970) computed the heritability of temperament (0.53).

Age, experience, sex, breed and handling are the major factors that influenced temperament and its relationship to body measurements of cattle in traditional farming systems. Some studies have reported a significant sex effect on temperament traits. Females are always more excitable or difficult to handle, heifers had higher temperament scores than their steers, who were more docile than heifers (Stricklin et al., 1980; Voisinet et al., 1997 a,b; Lanier et al., 2000; Gauly et al., 2001). These results clearly show that temperament traits of cattle can be considered as governed by the same pool of genes between sexes, even though heifers may exhibit higher phenotypic and genetic variability for some traits.

Voisinet et al. (1997a) showed that increased (poorer) temperament scores resulted in decreased daily gains. Cattle that were quieter and calmer during handling had higher average daily gains than cattle that became agitated during routine handling. According to Tulloh (1961; cit. Takeuchi and Houpt, 2003), Herefords and Angus had better temperament scores than Shorthorns. Animals with high temperament scores had significantly lower body weights than those with low temperament scores.

Genetic correlations suggested in Japanese Black cows that shorter and fatter cows had a better temperament than taller animals, and the h^2 for temperament score was 0.27 (Oikawa et al., 1989). The value may have been reduced by inclusion of factors such as pregnancy, type of management and quality of stockmanship in the estimation of the error variance.

Burrow (1997) reported that in *B. indicus*-derived cows with poor temperament scores were poor in milk yielding and had the poorest milking ability, the longest milking and let-down times and short lactations; docile animals yielded significantly more milk per milking, with the best milking ability in the shortest milking time. In other studies using *B. taurus* breeds, no significant relationship was found between temperament and milk yield (Takeuchi and Houpt, 2003). Correlation between temperament and milking speed was 0.36, between temperament and FCM (fat-corrected milk) of 0.19 and a final score of 0.36. The authors found higher genetic correlations than phenotypic correlations. According to Maffei et al. (2006), the correlations between reactivity and temperament score were 0.82 and 0.85. The values indicated that animals classified with higher reactivity also showed to be more aggressive in temperament, demonstrating the high degree of association between reactivity and temperament score.

Heritability of temperament in Japanese Black and Japanese Shorthorn cattle was 0.45 (paternal half-sibs) and 0.67 (mother-daughter pairs). It suggests the maternal effects on temperament (Sato, 1981). According to Shrode and Hammack (1971; cit. Hohenboken, 1987), differences among sire groups in Angus gave a heritability of 0.40 for the trait. Heritability of handling in a squeeze chute in purebred bulls was 0.48 and 0.44 in crossbred calves (paternal half-sib correlations) (Stricklin et al., 1980). The heritability of temperament score of *B. taurus* calves (Hereford, Simmental and Friesian) was 0.23 - 0.28, for *B. indicus*-sired calves (Brahman, Braford and Africander) was 0.46 - 0.37 (Hearnshaw and Morris, 1984). Morris et al. (1994) recorded significant differences in temperament among Angus and Hereford breeds and various crossbred groups. Heritable effects were generally low to moderate, for the average cow it was 0.22 (based on 176 sires), for the average yearling 0.32 (47 sire groups), and for the average calf 0.23 (53 sire groups).

Social behaviour

The basis of a social hierarchy is the mutual recognition of the animals. According to Sambraus (1975), up to 70 animals in a herd may recognize each other. Dominance in cattle depends on age, weight, sex, breeds and presence of horns. Male calves aged 6 months dominate females of the same age (Bouissou, 1972). An advantage of social order is the low incidence of aggression. Dominant animals have been aggressive in the past to obtain their rank position but do not need to be aggressive any more. Beilharz and Zeeb (1982) concluded that the dominance relationship is a result of learning; once learnt it persists for a long time. Sato et al. (1991) found significant correlations between social licking and milk yield: 0.65 for receiving licking, 0.55 for emitting licking and dominance value of 0.88. Broom and Leaver (1978) observed that young Friesian heifers showed more associations when they were reared as calves in the same group than existed between members of different groups. They also found that animals close together in the rank order were more likely to associate with each other (Takeuchi and Houpt, 2003).

Animals gain in dominance values up to the age of about 9 years in mixed-age herds, then cows show progressive decline in dominance values (Reinhardt and Reinhardt, 1975; Beilharz and Zeeb, 1982). According to Sambraus (1975), the ranking index increased up to an age of 10 years and remained on this level up to the age of 13 years. Burrow (1997) found that heritability estimates are higher in young animals and the variation in temperament scores is larger; in older animals they are reduced, because of additional handling.

Wagnon et al. (1966) confirmed the dominance of Angus over Shorthorns and of Shorthorns over Herefords for both years. Within breeds, dominance rank and weight were positively correlated; among breeds, this relationship was negative. Angus cows dominated Herefords (despite being lighter in weight), and that in groups, Angus tended to occupy central positions whereas Herefords were found on the periphery of the group (Stricklin, 1983). For several measures of spacing behaviour, distances from Angus cows to other cows were closer than those from Hereford cows to their neighbours. British-breed cattle were more docile than continental European-breed cattle. The breed ranking after introducing cows into established groups was Brown Swiss over Holstein, Guernsey, Ayrshire, and over Jersey. The average number of agonistic encounters also differed among breeds, but the rank (Ayrshire, Holstein, Jersey, Brown Swiss, Guernsey) was not related to body weight (Hohenboken, 1986). Brakel and Leis (1976) introduced cows into established herds of different breeds found that the breed ranking of Brown Swiss over Holstein over Guernsey over Jersey. In zebu Rathi cows, dominance ranks were correlated ($P < 0.05$) with first-lactation milk yield, indicating higher social ranks in high-producing cows. Dominance ranks were also highly correlated with heart girth and height at withers, in addition to body weight (Shiv-Prasad et al., 1996, cit. Takeuchi and Houpt, 2003).

The consistency of ranking between twin pairs was remarkable, with an intraclass correlation of 0.93 between twin pairs, indicating a strong genetic base for dominance (Purcell and Arave, 1991). Heritability of dominance h^2 (coefficient of heritability) was 0.4, indicating that the trait will respond to selection, but the value of selecting animals to change this trait should be assessed carefully (Beilharz et al., 1966). Dickson et al. (1970) found the heritability of social dominance near zero.

Significant correlations between social dominance and marching order to the milking parlour (0.49) or milking order (0.46) in a herd of cows with well-established social relationships were recorded (Lundberg et al., 1992). In contrast, Reinhardt (1978) did not find relations between the social order and the marching order to the daily grazing area in cattle. However, the position of the cows within the marching order was very constant. Takeuchi and Houpt (2003) noted correlations between rank position (determined by wins/losses) and aggressive (0.71), sexual (0.68) and vocal (0.61) behaviours. A result of this phenotypic correlation is the strong negative relationship between rank and sexual behaviour. Limited space does not allow the animals to perform all aspects of social behaviour and can result in aggressive interactions (Menke et al., 1994). In dairy cows a much higher level of agonistic behaviour has been observed in indoors conditions than at pasture (Takeuchi and Houpt, 2003). The heritability for aggressive activities was estimated by Bähr et al. (1984), as displacements from an automatic feeding dispenser (0.28) and, as displacements from cubicles (0.48). The level of aggression also appears to differ among breeds.

The heritability behavior results depended on the experimental design, different tests and scoring systems and previous experiences of the animals. Another reason for different heritability estimates can be found if animals are culled because of a striking temperament; the variance has changed and heritability estimates are reduced.

There is little evidence in the literature of effects of major genes on behavioural traits of livestock. Holmes et al. (1972, cit. Hohenboken, 1986), however, reported that cattle homozygous for double muscling or muscular hypertrophy were more temperamental than heterozygotes, which were more temperamental than homozygous normal individuals. The homozygous double-muscled animals were said to be more fearful than aggressive (Hohenboken, 1987).

Maternal behaviour

The genetics of maternal behaviour in cattle is important for survival of the young. Improved maternal behaviour could increase the welfare of mother and offspring. Beef breeds show more intense maternal behaviour than dairy breeds, because calves from dairy cattle have been reared artificially for many generations and there has been no selection pressure for this behavioural trait (Takeuchi and Houpt, 2003).

A number of the dairy cows and dairy heifers were slow or completely failed to initiate this licking of their offspring. The beef cows stood quickly to the teat-seeking of their calves, whereas dairy heifers and dairy cows remained lying (Selman et al., 1970). Ewbank (1967) observed pairs of monozygous and dizygous twins, and individually born calves paired as artificial twins concluded that the association of pair mates at pasture may be controlled more by the rearing methods used on the twins than by the genetic background of the animals. Buddenberg et al. (1986) observed behaviour for attentiveness of a cow to her calf and aggressiveness towards the caretaker. Angus cows scored lowest for maternal behaviour. Hereford, Charolais and Red Poll cows were similar in their mean maternal rating. Angus cows were more attentive to their calves and more aggressive to caretakers.

According to Broadhurst (1960; cit. Takeuchi and Houpt, 2003), maternal effects can influence temperament, but they are not great enough to completely change the temperament of a cross-fostered animal which has a temperament that is very different from that of the foster mother.

Development of emotional reactivity of the nervous system begins during early gestation. The handling the pregnant mother had the opposite effect on the behaviour of the young. Handling and possibly stressing the pregnant mothers changed the hormonal environment of the foetus which resulted in nervous offspring (Grandin and Deesing, 1998). Roussel et al. (2004) showed that stress in pregnant animals affects the subsequent reactivity of their offspring.

CONCLUSION

Because environmental factors have a large influence on behaviour, it is also necessary to integrate the hypothetical interactions between the genotype of animals and the characteristics of the farming environment. Likewise, it is imperative to evaluate the potential consequences of such selections on other desirable productive traits. Finally, recent molecular genetic tools may be applied in cattle to identify individual genes or markers for these genes known to influence behaviour especially fearfulness. Such future approaches open a way forward to enhance our ability to select directly for such genes rather than relying on behavioural phenotypes, particularly for traits where the phenotype is difficult to measure. The values of the heritability estimates indicate that most of the traits would respond to selection. Breeding programmes selecting special performance traits could include the effects on behaviour. However, behavioural traits have polygenic inheritance and selecting one trait may change other traits. Before behavioural traits are included in breeding programmes, the complete effects for the population should be carefully assessed.

Clearly defined genetic parameters are needed, which are based on sufficient numbers of animals included in the samples. It can be expected that molecular genetics will come up with interesting new results, identifying special genes for each individual behavioural trait, and collaboration between ethologists and geneticists will find interesting new aspects in this branch of science.

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