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Temperament and productivity in beef cattle

Temperament traits of beef calves measured under field conditions and their relationships to performance¹

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ABSTRACT

A total of 3050 German Angus (Aberdeen Angus x German dual-purpose breeds), Charolais, Hereford, Limousin and German Simmental calves were used to examine temperament traits of beef cattle using two different test procedures. Both, the crush test and the flight-speed test have been validated in terms of routine on-farm applicability. Behavior tests were performed in 2006 and 2007 on 24 commercial beef cattle farms located in the northern and eastern part of Germany. A single, trained observer assigned subjective scores to characterize the behavior of each animal during restraint in the head gate (calm, restless shifting, squirming, vigorous movement, violent struggling) and when leaving the crush (walk, trot, run, jumping out of the crush). Breed was a significant source of variation in crush scores and flight-speed scores ($P < 0.001$). Charolais and Limousin cattle had the highest scores in both traits, whereas Herefords had the lowest crush scores. German Angus and Hereford calves had the lowest flight-speeds, indicating that these breeds have a more favorable temperament. Temperament scores differed significantly between male and female calves ($P < 0.01$), with females scored higher for both traits. Average daily weight gains of the calves were significantly influenced by effects of breed ($P < 0.001$) and sex ($P < 0.001$) of the calves. Heritabilities were estimated for crush- and flight-speed scores of beef cattle. They were lowest for crush score and flight-speed score of Limousin cattle with values of 0.11. In contrast, highest heritabilities were 0.33 for crush score, and 0.36 for flight-speed score of Hereford cattle. Genetic correlations were estimated among both temperament traits, with values between 0.57 and 0.98. Crush scores and visual flight-speed scores were negatively correlated with daily weight gain of the calves in most breeds. The results presented in this paper point out that on-farm evaluation of beef cattle temperament is possible, either using the crush test or the flight-speed test. Genetic selection seems to be promising to

improve temperament traits of beef cattle without decreasing production traits like average daily weight gain of the calves.

Key Words: beef cattle, behavior test, flight-speed, production traits, temperament

INTRODUCTION

Beef cattle are usually kept under extensive rearing conditions, partially on pasture throughout the year and with a decreased labor input per animal (Le Neindre et al., 1998). Close human-animal interactions are restricted to veterinary care or routine management procedures and are associated with stress for the animals (Rushen et al., 1999). Due to the limited habituation to men, negative behavioral responses of beef cattle are likely to happen more often during handling, strengthening the risk of injuries or increasing the workload for cattle handling (Le Neindre et al., 2002).

The behavioral response of beef cattle to human handling was chosen as an indicator for an animal's temperament (Grandin, 1993; Burrow, 1997). It can vary from docility to aggression, with docility being preferred for farming conditions. Temperament can be quantified by scoring behavior in a standardized test situation (Tulloh, 1961; Burrow et al., 1988; Le Neindre et al., 1995; Hoppe et al., 2008).

Temperament differs among beef cattle breeds and gender (Stricklin et al., 1980; Vanderwert et al., 1985; Gauly et al., 2001a, b). It has been shown to be related to various aspects of animal production, such as daily weight gain, feed conversion and beef quality (Fordyce et al., 1988; Voisinet et al., 1997; Colditz et al., 1999; Petherick et al., 2002; Nkrumah et al., 2007).

Heritabilities of temperament are low to moderate (Morris et al., 1994; Burrow and Corbet, 2000; Mathiak, 2002), indicating the possibility to include temperament in an overall breeding goal.

The purpose of this study was to determine most relevant environmental factors affecting temperament of the most common beef cattle breeds in Germany. For the first time, both the crush test and the flight-speed test have been validated in terms of routine on-farm applicability.

Estimation of genetic (co)variance components among temperament and production traits was accomplished to generate a base for future selection strategies.

MATERIALS AND METHODS

Experimental location

The present study was conducted in 2006 and 2007 on 24 commercial beef cattle farms located in the northern and eastern part of Germany. Completeness of performance and pedigree data was ensured by selecting beef cattle herds in cooperation with the responsible breeding associations.

Animals

Beef cattle used in this study originated from the following five beef cattle breeds: German Angus (Aberdeen Angus x German dual-purpose breeds), Charolais, Hereford, Limousin and German Simmental. In total, 3050 calves were tested at an average age of $233\text{d} \pm 68\text{d}$ (Table 1). An overview of the genetic structure within each breed is given in Table 2. Main differences between numbers of tested animals on the farms are presented in Table 3. The large range is due to some farms where only a part of the herd could be tested.

Test procedures

Temperament of calves was scored using the crush-test (mod. from Tulloh, 1961). Crush scores reflect the animal's behavior while restraint in the head gate, and were assigned immediately after fixation. Crush scores for all animals were given by the same observer, according to a five-point system suggested by Grandin (1993): 1 = calm, no movement; 2 = restless, shifting; 3 = squirming, occasionally shaking of the crush; 4 = continuous vigorous movement, and shaking of the crush; 5 = rearing, twisting of the body, or violent struggling. Additionally, the same observer recorded the gait of the calves while leaving the crush and a visual flight-speed score

was assigned to each calf. According to Lanier and Grandin (2002), the flight-speed scores were: 1 = walk; 2 = trot; 3 = run, and 4 = jumping out of the crush.

For each animal, the rank order of entrance into the crush was recorded. Due to different group sizes, the absolute rank order was transformed to a relative rank order using the following formula:

$$\text{Relative rank order} = \frac{\text{absolute rank order}}{\text{absolute group size}} \times 100\%$$

According to their relative rank order, animals were distributed in five different groups for rank order as follows: 1 = 1% - 20%; 2 = 21% - 40%; 3 = 41% - 60%; 4 = 61% - 80%; 5 = 81% - 100%.

During restraint in the crush, the body-weight of each animal was measured. Average daily weight gain of the calves was calculated for the time interval from birth to testing date, using birth weight corrected body weights.

Statistical analysis

Analysis of variance to reveal the impact of environmental effects on traits was carried out with the software package SAS 9.1.3 (2001) using the Mixed procedure.

The temperament traits crush score and flight-speed score were analyzed using the following model 1:

$$y_{ijklmn} = \mu + B_i + S_j + Y_k + F_l(B_i) + G_m + bA + e_{ijklmn} [1]$$

with y_{ijklmn} = observed trait, μ = overall mean, B_i = fixed effect of breed, S_j = fixed effect of sex, Y_k = fixed effect of year, $F_l(B_i)$ = fixed effect of farm within breed, G_m = fixed effect of rank order group, bA = age of animal as linear regression, and e_{ijklmn} = random residual effect.

The following model 2 was used to analyze body-weight and average daily weight gain (ADG):

$$y_{ijklm} = \mu + B_i + S_j + Y_k + F_l(B_i) + bA + e_{ijklm} [2]$$

with y_{ijklm} = observed trait, μ = overall mean, B_i = fixed effect of breed, S_j = fixed effect of sex, Y_k = fixed effect of year, $F_l(B_i)$ = fixed effect of farm within breed, bA = age of animal as linear regression, and e_{ijklm} = random residual effect.

Estimation of genetic (co)variance components among crush score, flight-speed score, and average daily weight gain, was done using a multivariate animal model for REML and applying the package VCE 4.0, Version 4.2.5 (Neumeier and Groeneveld, 1998). This was done separately for each breed. Pedigrees were traced back for three generations. For genetic analysis, the statistical model for the three traits in matrix notation was:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \\ \mathbf{y}_3 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 & 0 \\ 0 & \mathbf{X}_2 & 0 \\ 0 & 0 & \mathbf{X}_3 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \\ \mathbf{b}_3 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & 0 & 0 \\ 0 & \mathbf{Z}_2 & 0 \\ 0 & 0 & \mathbf{Z}_3 \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \mathbf{a}_3 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \mathbf{e}_3 \end{bmatrix}$$

where

\mathbf{y}_i = vector of observations for the i th trait, \mathbf{b}_i = vector of the fixed effects for the i th trait, \mathbf{a}_i = vector of random genetic animal effects for the i th trait, \mathbf{e}_i = vector of random residual effects for the i th trait, and \mathbf{X} and \mathbf{Z} are the incidence matrices relating records to fixed and random effects.

The fixed effects in the model were sex, farm, year, and the age of the animal.

The corresponding matrix of variances and covariances for random effects was:

$$\text{var} \begin{bmatrix} a_1 \\ a_2 \\ a_3 \\ e_1 \\ e_2 \\ e_3 \end{bmatrix} = \begin{bmatrix} g_{11}A & g_{12}A & g_{13}A & 0 & 0 & 0 \\ g_{21}A & g_{22}A & g_{23}A & 0 & 0 & 0 \\ g_{31}A & g_{32}A & g_{33}A & 0 & 0 & 0 \\ 0 & 0 & 0 & r_{11} & r_{12} & r_{13} \\ 0 & 0 & 0 & r_{21} & r_{22} & r_{23} \\ 0 & 0 & 0 & r_{31} & r_{32} & r_{33} \end{bmatrix}$$

where

g_{ij} = the elements of **G**, the additive genetic variance and covariance matrix among the three traits for animal effects, and r_{ij} are the elements of **R**, the variance and covariance matrix for residual effects.

RESULTS

Breed differences were highly significant ($P < 0.001$) for crush scores and flight-speed scores (Table 4). Charolais and Limousin calves had the highest crush scores with values of 2.78 ± 0.06 and 2.95 ± 0.07 , respectively. Intermediate crush scores were observed in German Angus and German Simmental cattle (Figure 1). Herefords had the lowest crush scores (2.05 ± 0.07). German Angus and Hereford calves had the lowest flight-speeds, with values of 1.49 ± 0.05 and 1.46 ± 0.06 , respectively. A continuous and significant increase in flight-speed scores were observed for German Simmental, Charolais and Limousin cattle (Figure 2).

Temperament scores differed significantly between male and female calves ($P < 0.01$). Females had a crush score of 2.57 ± 0.03 , and a flight-speed score of 1.69 ± 0.03 . In contrast, male calves were scored 2.49 ± 0.03 and 1.58 ± 0.03 for both traits. Corresponding values within each breed are presented in Table 5. In 2006, the animals' behavior was more agitated during handling compared to lower scores in 2007 (Table 5). Only Hereford and Limousin cattle had lower flight-speed scores in the second year of this trial. Both measurements of temperament were significantly influenced by the effect of farm within breed ($P < 0.001$).

The subjective behavior scores of the animals during restraint in the head gate and when exiting the crush were positively associated with increases in the class relative rank order ($P < 0.001$). Calves having low scores for the relative rank order had lower crush scores ($P < 0.001$) compared to animals of rank order groups 2 - 5 (Figure 3). Later entering of an animal in the

weighing crush was associated with higher flight-speed scores ($P < 0.005$). Calves in group 5 for relative rank order had the highest scores, indicating that they were more likely to run fast out of the crush if the front door was opened (Figure 4).

Average daily weight gains of the calves were significantly influenced by effects of breed ($P < 0.001$) and sex ($P < 0.001$) of the calves (Table 6). Male calves had higher average daily weight gains within each breed compared to female calves. Highest average daily weight gains were recorded for German Simmental cattle, with values of 1231 g/d and 1092 g/d for male and female calves, respectively, followed by Charolais and Hereford cattle. Average daily weight gain was lowest for German Angus calves.

Heritabilities were estimated for crush- and flight-speed scores of beef cattle. Estimates differed between 0.11 and 0.36 (Tables 7, 8). Heritabilities of crush score and flight-speed score were lowest for Limousin cattle having values of 0.11. In contrast, highest heritabilities were 0.33 for crush score, and 0.36 for flight-speed score of Hereford cattle. Genetic correlations were estimated between both traits of temperament, with values between 0.57 and 0.98 (Table 9). Both crush score and visual flight-speed score were negatively correlated with daily weight gain of the calves in most breeds (Table 9).

DISCUSSION

In this study, German Angus and Hereford cattle received lowest behavior scores in both temperament tests, indicating a calmer temperament of animals of these breeds compared to Charolais, Limousin, or German Simmental. Beneficial behavioral traits of British breeds were already observed in former studies (Vanderwert et al., 1985; Burrow and Corbet, 2000; Baszczak et al., 2006). Gauly et al. (2001a) found that German Angus cattle were easier to handle during a

docility test than German Simmentals. Charolais and Limousin cattle seem to be more susceptible for stress during social isolation and close human-animal interaction, resulting in higher behavioral agitation during restraint, and higher flight-speeds when leaving the crush. The breeding history of Charolais and Limousin cattle may be an explanation for their excitable temperament. The traditional French rearing system with a strong habituation of cattle to men could have masked underlying temperament traits preventing indirect selection processes (Grandin, 1994; Grandin et al., 1995). In contrast, Angus and Hereford cattle are traditionally reared under extensive pasture conditions with a minimum of human-animal-interactions. This may have promoted an indirect selection of calm and docile animals, whereas very nervous and aggressive animals were culled. This is also true for German Angus cattle, developed in the 1950s by breeding Aberdeen Angus bulls to German dual-purpose breeds. Repeated mating of Aberdeen Angus bulls to the initial population of German Angus cows may have forwarded docility of today's German Angus cattle.

Apart from the crush scores of Charolais cattle, female calves were scored higher in both test situations compared to male calves from the same breed, although not all differences were significant ($P > 0.05$). Based on these results, it could be assumed that at this age, male cattle have a more favorable temperament and are easier to handle than their female counterparts. This is in accordance with former studies observing higher behavioral agitation of female cattle during human handling (Stricklin et al., 1980; Voisinet et al., 1997; Gauly et al., 2001b). Temperament scores were higher in the second year of this trial. It is possible that different environmental influences like weather and resultant modifications of herd- and pasture management, e.g. frequent change of pasture and supplementary feeding, associated with habituation to human handling may have altered behavior of the animals. In addition, cattle used

in this study were sired by different bulls (Table 2), with some bulls having progeny only in 2006 or 2007. Le Neindre et al. (1995) studied docility of Limousin heifers sired by 34 bulls, with significant differences between progeny groups. Similar results were reported by Mathiak (2002) for temperament traits of German Angus and German Simmental cattle sired by different bulls. Relating to these results, sire effects may partially explain the effect of year in this study.

As expected, the influence of farm within each breed effect on temperament traits was highly significant ($P < 0.001$), indicating that factors like prior experiences with human contact or handling, herd- and pasture management may have altered behavior patterns of the calves. Lanier et al. (2000) observed behavioral agitation of beef cattle during commercial auctions. They stated that it was not possible to control all the variables contributing to temperament differences. This may be the same for the impact of different management effects in this study, described in the model by the general farm effect.

The behavioral agitation of the animals during fixation in the crush and the flight-speed were significantly influenced by the group of relative rank order, with calves of the first group having the lowest crush- and flight-speed scores. Calves which were easy to drive into the handling facility, or even passed it voluntarily, were more likely to remain calm and docile during restraint in the head gate. This finding confirms a former study by Tulloh (1961). Using *Bos indicus* crossbreeds, Orihuela and Solano (1994) observed the relationship between order of entry and time spent to cover a distance of 20m in a slaughterhouse. They found that animals at the beginning of each group of five to seven cattle traversed the runway more quickly, indicating that they were easier to handle. In sheep, Syme and Elphick (1982) observed that vocal and stubborn animals moved at the back of the group during handling. Selecting calm and docile animals could therefore facilitate cattle handling, associated with reduced workload for routine

management procedures. However, other factors may have contributed to the higher behavioral agitation of animals which were tested at the end of the whole group, e.g. they were separated from the herd for a long period of time (Grandin, 1980).

Body weight at testing date and average daily weight gain were significantly influenced by effects of breed ($P < 0.001$) and sex ($P < 0.001$) of the calves. This is in accordance with results of a former study using German Angus and Simmental cattle (Hoppe et al., 2008). Performance traits of the tested animals are representative for each breeds population in Germany (BDF, 2007).

Heritabilities estimated for both behavioral traits are low to moderate with significant differences between breeds. These estimates correspond with those reported earlier by Burrow and Corbet (2000). For repeated handling in a crush, Mathiak (2002) estimated heritabilities between 0.18 and 0.43 for German Angus and between 0.05 and 0.30 for German Simmental, respectively. Genetic correlations between both measurements of temperament differ between 0.57 in German Angus cattle and 0.98 in Limousin and German Simmental cattle. According to these results, it seems that either crush test or observation of flight-speed measure the same aspects of temperament. In this experiment, beef cattle calves were exposed to social isolation from their herdmates, and close human contact during restraint in the crush, which have generated individual reactions of the calves to the test procedure. Both higher behavioral agitation during restraint and higher flight-speed scores indicate an attempt to escape in this restricted test situation. Therefore it is possible to use both tests to evaluate cattle temperament. Heritability is generally higher for visual flight-speed scores in contrast to crush scores. Consequently, recording the gait of cattle exiting the crush may be a less subjective and more accurate measurement of temperament than the crush test. When applying the crush test, the observer

assigns a score to the degree of agitation during restraint (Baker et al., 2003) associated with a highly subjective component. The negative genetic correlations between average daily weight gain and temperament scores suggest that less docile animals are less productive. Selection of beef cattle with desirable temperaments may lead to increased performance, resulting in both economic improvement of beef cattle production as well as labor efficiency due to improvements in behavior.

The results of this study show that both the crush-test and flight-speed scoring are adequate tools to detect individual differences in beef cattle temperament under field conditions. In terms of the requirements for a good test procedure devised by Grignard et al. (2001) and Boivin and Trillat (2006), these tests are easy to perform on farm. In addition, moderate heritabilities of both traits indicate sufficient repeatability. Furthermore, the crush test used in this study corresponds to routine handling situations representing current beef cattle husbandry conditions, because many routine management tasks are performed in a crush. The integration of both tests in the routine weighing process at weaning prevents additional workload for cattle handling and further stress for the animals. Another advantage of visual flight-speed scores is that no further equipment is required as it is the case in electronic measurement of the time interval for a fixed distance after leaving the weighing crush (Burrow et al., 1988). Electronic measurement of flight-speed is a more cost-intensive procedure but an advantage is that these measures are more objective and recorded on a continuous scale yielding to higher heritabilities.

The results presented in this paper clearly point out that on-farm evaluation of beef cattle temperament is possible, either using the crush test or the flight-speed test. Genetic selection to improve temperament traits of beef cattle without decreasing production traits like average daily weight gain of the calves seems to be promising. Within Hereford, Limousin and German

Simmental cattle, a simultaneous improvement of temperament and performance can be expected.

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Table 1. Number of calves by breed and sex tested for temperament in 2006 and 2007, and average age (\pm SD) of calves at testing

Item	German Angus	Charolais	Hereford	Limousin	German Simmental
2006					
Male	219	124	188	138	209
Female	207	130	185	125	130
2007					
Male	149	158	165	72	156
Female	131	144	159	89	172
Total	706	556	697	424	667
Age (d)	278 \pm 63	263 \pm 72	194 \pm 42	233 \pm 69	202 \pm 49

Table 2. Number of sires and offspring per sire within breeds

Breed	Number of sires	Offspring per sire	
	n	Mean (\pm SD)	Range
German Angus	40	17.6 \pm 19.1	1 – 73
Charolais	32	17.4 \pm 16.7	1 – 64
Hereford	40	17.4 \pm 20.4	1 – 80
Limousin	56	7.6 \pm 8.6	1 – 45
German Simmental	45	14.8 \pm 18.2	1 – 89

Table 3. Number of farms and tested animals per farm within breeds

Breed	Number of farms ¹	Tested animals per farm	
	n	Mean (\pm SD)	Range
German Angus	6	117.7 \pm 44.6	36 – 167
Charolais	4	139.0 \pm 23.8	119 – 137
Hereford	5	139.4 \pm 131.5	25 – 343
Limousin	6	70.7 \pm 44.3	29 – 151
German Simmental	6	111.2 \pm 93.5	12 – 256

Table 4. Significances of fixed effects in the analyses of temperament traits

Fixed effect	Crush score	Flight-speed score
Breed	$P < 0.001$	$P < 0.001$
Sex	$P = 0.0085$	$P < 0.001$
Year	$P < 0.001$	$P = 0.0079$
Farm within breed	$P < 0.001$	$P < 0.001$
Rank order group	$P < 0.001$	$P < 0.001$

Table 5. Least-square means (\pm SE) for crush score and flight-speed score stratified by the effects of sex of calf and year

Test	Item	German Angus	Charolais	Hereford	Limousin	German Simmental
	Sex					
Crush score	male	2.48 \pm 0.07	2.79 \pm 0.07	1.98 \pm 0.08	2.92 \pm 0.08	2.27 \pm 0.08
	female	2.57 \pm 0.07	2.77 \pm 0.07	2.13 \pm 0.08	2.99 \pm 0.08	2.40 \pm 0.08
Flight-speed	male	1.46 \pm 0.06	1.67 \pm 0.06	1.40 \pm 0.06	1.69 \pm 0.07	1.73 \pm 0.07
	female	1.51 \pm 0.06	1.78 \pm 0.06	1.52 \pm 0.06	1.87 \pm 0.07	1.89 \pm 0.07
	Year					
Crush score	2006	2.38 \pm 0.05	2.54 \pm 0.07	1.97 \pm 0.08	2.84 \pm 0.07	2.22 \pm 0.09
	2007	2.57 \pm 0.06	2.92 \pm 0.07	2.17 \pm 0.08	3.06 \pm 0.10	2.55 \pm 0.10
Flight-speed	2006	1.40 \pm 0.04	1.50 \pm 0.06	1.53 \pm 0.06	1.84 \pm 0.06	1.68 \pm 0.08
	2007	1.45 \pm 0.04	1.81 \pm 0.06	1.48 \pm 0.07	1.73 \pm 0.08	1.80 \pm 0.08

Table 6. Least-square means (\pm SE) for weight and average daily weight gain (ADG) at testing date stratified by the effects of breed and sex of the calves

Breed	Sex	Weight (kg)	ADG (g/d)
German Angus	male	337 \pm 2.2	1099 \pm 8
	female	297 \pm 2.3	963 \pm 9
Charolais	male	363 \pm 2.7	1216 \pm 10
	female	326 \pm 2.7	1089 \pm 10
Hereford	male	272 \pm 2.2	1210 \pm 12
	female	244 \pm 2.2	1081 \pm 12
Limousin	male	292 \pm 2.9	1130 \pm 12
	female	258 \pm 2.7	1004 \pm 11
German Simmental	male	284 \pm 2.6	1231 \pm 13
	female	255 \pm 2.7	1092 \pm 14

Table 7. Estimated variance components and heritability estimates (\pm SE) of crush score of the calves

Variance component	German Angus	Charolais	Hereford	Limousin	German Simmental
σ^2 additive-genetic	0.122	0.140	0.267	0.094	0.169
σ^2 residual	0.692	0.669	0.541	0.756	0.746
σ^2 phenotypic	0.814	0.809	0.808	0.850	0.915
h^2 (\pm SE)	0.15 ± 0.06	0.17 ± 0.07	0.33 ± 0.10	0.11 ± 0.08	0.18 ± 0.07

Table 8. Estimated variance components and heritability estimates (\pm SE) of flight-speed score of the calves

Variance component	German Angus	Charolais	Hereford	Limousin	German Simmental
σ^2 additive-genetic	0.066	0.124	0.159	0.058	0.171
σ^2 residual	0.267	0.380	0.282	0.459	0.450
σ^2 phenotypic	0.333	0.504	0.441	0.517	0.621
h^2 (\pm SE)	0.20 ± 0.08	0.25 ± 0.10	0.36 ± 0.06	0.11 ± 0.07	0.28 ± 0.07

Table 9. Genetic correlations (\pm SE) among crush score (CS), flight-speed score (FS) and average daily weight gain (ADG) of the calves

Breed	CS – FS	CS – ADG	FS – ADG
German Angus	0.57 ± 0.17	-0.13 ± 0.22	-0.04 ± 0.12
Charolais	0.63 ± 0.12	-0.16 ± 0.12	-0.29 ± 0.17
Hereford	0.69 ± 0.08	-0.58 ± 0.11	-0.37 ± 0.11
Limousin	0.98 ± 0.08	-0.27 ± 0.27	-0.41 ± 0.27
German Simmental	0.98 ± 0.05	-0.34 ± 0.18	-0.27 ± 0.14

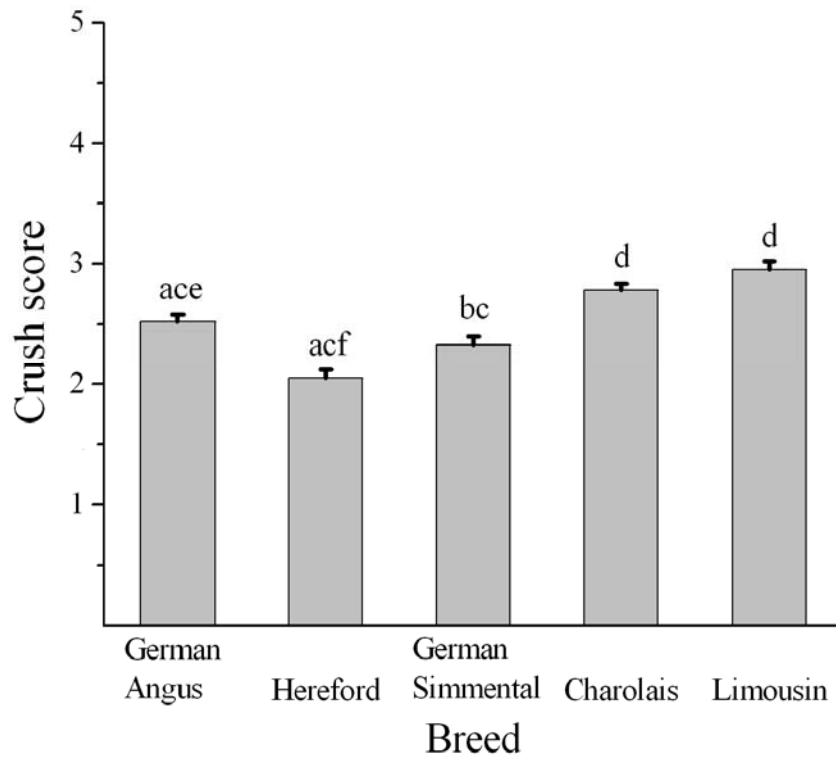


Figure 1. Least-square means (\pm SE) for crush score by the effect of the breed a,b; c,d; e,f: $P < 0.05$

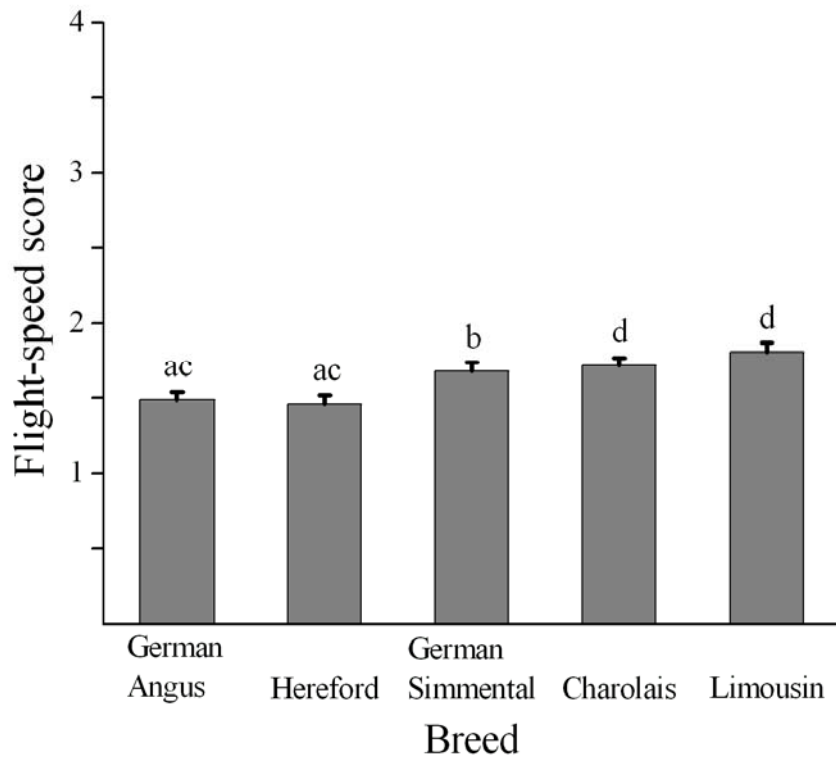


Figure 2. Least-square means (\pm SE) for flight-speed score by the effect of the breed
a,b; c,d: $P < 0.05$

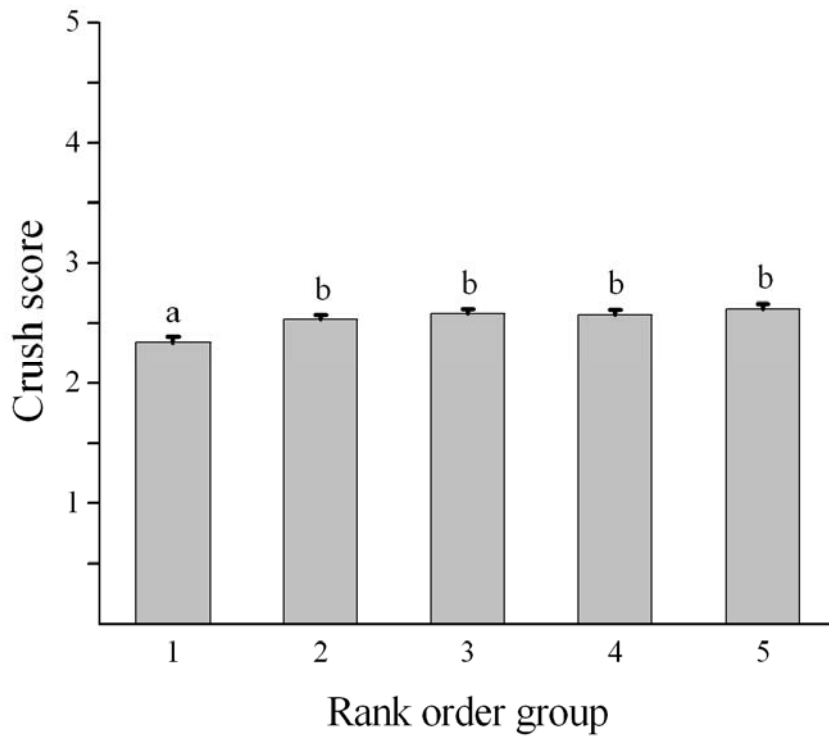


Figure 3. Least-square means (\pm SE) for crush score by groups for relative rank order a,b: $P < 0.001$

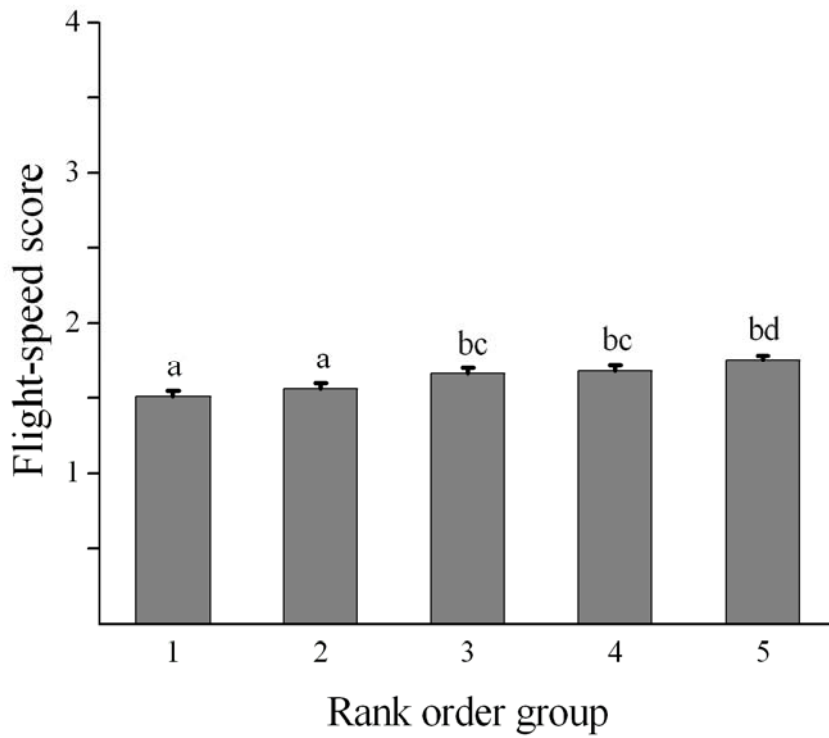


Figure 4. Least-square means (\pm SE) for flight-speed score by groups for relative rank order a,b; c,d: $P < 0.05$