

Effects of inbreeding on number of piglets born total, born alive and weaned in Austrian Large White and Landrace pigs

ASTRID KÖCK, BIRGIT FÜRST-WALTL and ROSWITHA BAUMUNG

Division Livestock Sciences, University of Natural Resources and Applied Life Sciences Vienna (BOKU), Vienna, Austria

Abstract

In this study records of 58 925 litters of Austrian Large White and 17 846 litters of Austrian Landrace pigs were analysed. Regression models were used to determine the effects of litter, dam and sire inbreeding on total number of born, born alive and weaned piglets in Large White and Landrace. In both populations, litter and dam inbreeding showed a negative effect on all traits. Sire inbreeding had no effect in Large White, whereas a significant positive effect was observed in Landrace. On average, inbred sires with an inbreeding coefficient of 10% had 0.45 more piglets born total and 0.43 more piglets born alive in comparison to non-inbred sires. In a further analysis the total inbreeding coefficients of the animals were divided into two parts: »new« and »old« inbreeding. »New« inbreeding was defined as the period of the first five generations. It was shown that the observed inbreeding effects were not only caused by recent inbreeding. Reproductive performance was also affected by »old« inbreeding. Finally partial inbreeding coefficients of four important ancestors in each population were calculated to investigate if inbreeding effects are similar among these ancestors. The results revealed a variation of inbreeding effects among the four ancestors. Alleles contributing to inbreeding depression were descendent from specific ancestors.

Keywords: inbreeding effects, pigs, litter size, age of inbreeding, heterogeneity of inbreeding depression

Zusammenfassung

Einfluss der Inzucht auf Anzahl gesamt geborener, lebend geborener und hochzogener Ferkel bei Edelschwein und Landrasse

In dieser Studie standen 58 925 Wurfdaten beim Edelschwein und 17 846 Wurfdaten bei der Landrasse zur Verfügung. Mit Regressionsmodellen wurde der Einfluss der Inzuchtkoeffizienten von Ferkel, Sau und Eber auf die Anzahl gesamt geborener, lebend geborener und hochzogener Ferkel untersucht. In beiden Populationen wirkten sich Ferkel- und Saueninzucht negativ auf die Fruchtbarkeitsmerkmale aus. Beim Edelschwein hatte Eberinzucht keinen Einfluss auf die Zuchtleistung, während bei der Landrasse ein positiver Inzuchteffekt festgestellt wurde. Eber mit einem Inzuchtkoeffizienten von 10% haben um 0,45 mehr gesamt geborene und 0,43 mehr lebend geborene Ferkel als nicht ingezüchtete. In einer weiteren Analyse wurden die Inzuchtkoeffizienten in »junge« und »alte« Inzucht

unterteilt, wobei »junge« Inzucht aus den ersten fünf Generationen in den Pedigrees stammt. Es wurde festgestellt, dass die beobachteten Inzuchteffekte nicht nur auf »junge« Inzucht zurückgehen. »Alte« Inzucht hatte ebenfalls einen Einfluss auf die Fruchtbarkeitsleistung. Weiters wurden partielle Inzuchtkoeffizienten für jeweils vier wichtige Ahnen beim Edelschwein und der Landrasse berechnet. Die Ergebnisse zeigten, dass die Auswirkung der Inzucht davon abhängt, auf welchen Ahnen sie zurückgeht. Allele, die zur Inzuchtdepression beitragen stammen von bestimmten Ahnen.

Schlüsselwörter: Inzuchteffekte, Schwein, Wurfgröße, Alter der Inzucht, Variation der Inzuchtdepression

Introduction

The decrease in performance of offspring of matings between close relatives is known as inbreeding depression. The first scientific evidence for inbreeding depression was published by DARWIN (1876) more than a century ago. Since then, the deleterious consequences of inbreeding were documented in many species (e.g. FALCONER & MACKAY 1996, HEDRICK & KALINOWSKI 2002, KELLER & WALLER 2002). Nevertheless, the mechanisms and effects of inbreeding are still not completely clear.

The genetic basis of inbreeding depression is explained by two main hypotheses. The first hypothesis, the partial dominance hypothesis (DAVENPORT 1908, CROW 1952), posits inbreeding depression as being caused by the expression of deleterious recessive alleles in the homozygous state. Inbreeding increases the frequency of homozygotes and thus deleterious recessive alleles, which are hidden in heterozygotes, will become increasingly expressed. The second is the overdominance hypothesis by EAST (1908) and SHULL (1908). Here inbreeding depression is attributed to the superiority of heterozygotes over both homozygotes. The reduced frequency of heterozygotes due to inbreeding will reduce opportunities to express this overdominance. In addition a third hypothesis has been suggested, which partly explains inbreeding depression as a consequence of a breakdown of epistatic interaction between loci (TEMPLETON & READ 1994).

Inbreeding does not affect all traits to the same degree. Inbreeding depression is most severe in traits that are closely related to fitness, e.g. offspring survival and fertility (FALCONER & MACKAY 1996, DE ROSE & ROFF 1999). DE ROSE & ROFF (1999) concluded that traits less closely related to fitness (e.g. adult body weight) exhibit little or no directional dominance.

Furthermore the effect of inbreeding in the same trait varies among species and populations within species (THORNHILL 1993, FRANKHAM *et al.* 2002). Recent studies revealed that inbreeding depression also shows variation among founders and lineages within a population (PRAY & GOODNIGHT 1995, LACY *et al.* 1996, RODRIGÁÑEZ *et al.* 1998, MIGLIOR *et al.* 1994, GULISIJA *et al.* 2006). Variability of inbreeding depression arises if founders or lineages of a population vary in number of deleterious recessive alleles (genetic load).

The objective of this study was to examine the effects of inbreeding on the important reproduction traits total number of piglets born, number of piglets born alive and number of weaned piglets in Austrian Large White and Landrace pigs by linear and quadratic

regression models and by splitting inbreeding into different inbreeding coefficients (total inbreeding coefficient of litter, dam and sire, »new« and »old« inbreeding, partial inbreeding coefficient).

Material and methods

Performance data

Field data for reproductive performance of purebred Austrian Large White and Austrian Landrace sows were available from 1967 to February 2007. The following information was recorded for each sow: identity number, herd, parity number, identity number of service sire, date of service, date of farrowing, farrowing interval, number of piglets born total, number of piglets born alive and number of piglets weaned. Records of sows with an age at first farrowing lower than 280 days and higher than 505 days and a gestation length lower than 105 days or higher than 125 days were deleted. Additionally litter records with a farrowing interval lower than 120 days or higher than 270 days were not considered in the analysis. After data editing, 58 925 litter records from 17 784 sows and 2 880 boars for Large White and 17 846 litter records from 7 568 sows and 1 840 boars for Landrace were available. A summary of recorded data is shown in Table 1.

Table 1

Means and standard deviations (SD) of the traits number of piglets born total, born alive and weaned of Large White and Landrace

Mittelwerte und Standardabweichungen (SD) für die Merkmale gesamt geborene, lebend geborene und hochgezogene Ferkel für Edelschwein und Landrasse)

Trait	Breed	Number of records	Mean	SD
Total number born	Large White	58 925	11.70	2.32
	Landrace	17 846	11.12	2.31
Number born alive	Large White	58 925	11.24	2.22
	Landrace	17 845	10.77	2.23
Number weaned	Large White	58 720	9.98	2.03
	Landrace	17 834	9.68	2.01

Pedigree data

Pedigrees of Large White and Landrace pigs contained information of animals born between 1965 and 2006. The pedigree files did not include all progeny of the sows in the reproductive performance data. Thus dummy progeny was created to get inbreeding coefficients for the litters in such cases. The entire pedigree contained the relationship of 102 896 animals for Large White and of 52 503 animals for Landrace.

Models

The effects of inbreeding on total number of piglets born, number of piglets born alive and weaned in Large White and Landrace were investigated with the procedure GLM of the software package SAS (SAS, Version 9.1, 2003). Different inbreeding coefficients were used to determine the effects of inbreeding. The following inbreeding coefficients and models were applied.

Total inbreeding coefficient

The overall effect of inbreeding was examined with the total inbreeding coefficient. The total inbreeding coefficient is defined as the probability that two alleles at any locus are identical by descent (WRIGHT 1922, MALÉCOT 1948).

Inbreeding coefficients were calculated with the algorithm of VANRADEN (1992) implemented in the software package PEDIG (BOICHARD 2002).

All traits were analyzed with the same model. Inbreeding coefficients of litter, dam and sire were defined as covariates. In model 1 linear regression coefficients of inbreeding were considered, whereas linear and quadratic regression coefficients were tested in model 2. Furthermore, parity number, herd-year class, farrowing season and age of the sow within parity number were included in the models.

$$Y_{ijkl} = \mu + pn_i + hy_j + season_k + b_1 age(pn_i) + b_2 F_l + b_3 F_d + b_4 F_s + \varepsilon_{ijkl} \quad (1)$$

$$Y_{ijkl} = \mu + pn_i + hy_j + season_k + b_1 age(pn_i) + b_2 F_l + b_3 F_l^2 + b_4 F_d + b_5 F_d^2 + b_6 F_s + b_7 F_s^2 + \varepsilon_{ijkl} \quad (2)$$

where Y_{ijkl} is the individual observation, μ the overall mean, pn_i the parity number i ($i=1-11$), hy_j the herd-year class j ($j=1-3$ 950 and 2 077 for Large White and Landrace, respectively), $season_k$ the farrowing season k ($k=1-6$), b_1-b_7 regression coefficients, $age(pn_i)$ the age of the sow within parity number, F_l the total inbreeding coefficient of the litter, F_d the total inbreeding coefficient of the dam, F_s the total inbreeding coefficient of the sire, ε_{ijkl} the residual error.

»New« and »old« inbreeding

The differences between effects of inbreeding evolved during recent generations compared to that evolved during the more distant past were investigated. For this analysis inbreeding coefficients of litter, dam and sire were split into two parts, corresponding to the inbreeding occurring in recent generations (»new«) and that which preceded it (»old«). »New« inbreeding was defined as the period of the first five generations.

The algorithm of VANRADEN (1992) in the programme PEDIG (BOICHARD 2002) was also used to compute inbreeding coefficients from the five most recent generations (parents, grand-parents etc.) in the pedigrees. These coefficients are called »new« inbreeding. »Old« inbreeding, however, resulted from the difference of the total inbreeding coefficient taking all available pedigree information into account and the »new« inbreeding of an animal. Generally, the correlation between »new« and »old« inbreeding was below 0.3.

Further »new« and »old« inbreeding coefficients of litter, dam and sire were considered separately in different models (3-5).

$$Y_{ijkl} = \mu + pn_i + hy_j + season_k + b_1 age(pn_i) + b_2 F_{l_new} + b_3 F_{l_old} + b_4 F_d + b_5 F_s + \varepsilon_{ijkl} \quad (3)$$

$$Y_{ijkl} = \mu + pn_i + hy_j + season_k + b_1 age(pn_i) + b_2 F_l + b_3 F_{d_new} + b_4 F_{d_old} + b_5 F_s + \varepsilon_{ijkl} \quad (4)$$

$$Y_{ijkl} = \mu + pn_i + hy_j + season_k + b_1 age(pn_i) + b_2 F_l + b_3 F_d + b_4 F_{s_new} + b_5 F_{s_old} + \varepsilon_{ijkl} \quad (5)$$

where Y_{ijkl} , pn_i , hy_j , $season_k$, $age(pn_i)$, F_l , F_d , F_s and ε_{ijkl} are defined as described above, while F_{l_new} is the young inbreeding of the litter, F_{l_old} the old inbreeding of the litter, F_{d_new} the young inbreeding of the dam, F_{d_old} the old inbreeding of the dam, F_{s_new} the young inbreeding of the sire, F_{s_old} the old inbreeding of the sire.

Partial inbreeding coefficient

To analyse whether the effects of inbreeding differ in magnitude and direction depending on the alleles' origin partial inbreeding coefficients were calculated. Inbreeding coefficients of each individual were partitioned into components due to certain ancestors. The partial inbreeding coefficient is defined as the probability that an individual is homozygous for an allele descended from a specified ancestor (LACY *et al.* 1996).

The most important ancestors of breeding animals born between 2003 and 2006 were determined for Large White and Landrace according to BOICHARD *et al.* (1997) using the programme PEDIG (BOICHARD 2002). Partial inbreeding coefficients of four genetically important ancestors with low relationship were calculated with the programme GRain (BAUMUNG *et al.* 2006) implemented in the software package PEDIG (BOICHARD 2007). The sum of the four partial inbreeding coefficients of an individual and the »rest« is equal to the total inbreeding coefficient of that individual. The »rest« is the part of the total inbreeding coefficient that will be explained by all other common ancestors.

The partial inbreeding coefficients of litter, dam and sire were again investigated using different models (6-8). The correlation between the partial inbreeding coefficients of ancestors did not exceed 0.5.

$$Y_{ijkl} = \mu + pn_i + hy_j + season_k + b_1 age(pn_i) + b_2 F_{l_A} + b_3 F_{l_B} + b_4 F_{l_C} + b_5 F_{l_D} + b_6 F_{l_Rest} + b_7 F_d + b_8 F_s + \varepsilon_{ijkl} \quad (6)$$

$$Y_{ijkl} = \mu + pn_i + hy_j + season_k + b_1 age(pn_i) + b_2 F_l + b_3 F_{d_A} + b_4 F_{d_B} + b_5 F_{d_C} + b_6 F_{d_D} + b_7 F_{d_Rest} + b_8 F_s + \varepsilon_{ijkl} \quad (7)$$

$$Y_{ijkl} = \mu + pn_i + hy_j + season_k + b_1 age(pn_i) + b_2 F_l + b_3 F_d + b_4 F_{s_A} + b_5 F_{s_B} + b_6 F_{s_C} + b_7 F_{s_D} + b_8 F_{s_Rest} + \varepsilon_{ijkl} \quad (8)$$

where Y_{ijkl} , pn_i , hy_j , $season_k$, $age(pn_i)$, F_l , F_d , F_s and ε_{ijkl} are defined as described above, while $F_{l_A} - F_{l_D}$ is the partial inbreeding coefficient of the litter due to ancestor A-D, F_{l_Rest} the remaining inbreeding coefficient of the litter, $F_{d_A} - F_{d_D}$ the partial inbreeding coefficient of the dam due to ancestor A-D, F_{d_Rest} the remaining inbreeding coefficient of the dam, $F_{s_A} - F_{s_D}$ the partial inbreeding coefficient of the sire due to ancestor A-D, F_{s_Rest} the remaining inbreeding coefficient of the sire.

Results

Inbreeding coefficients

Means, standard deviations and maximal values of different inbreeding coefficients for litters, dams and sires of Large White and Landrace in the reproductive performance data are shown in Table 2.

Table 2

Means (%), standard deviations (SD) and maximum values (%) of total inbreeding coefficients, »new« and »old« inbreeding and partial inbreeding coefficients due to four ancestors for litters, dams and sires in Large White and Landrace

Mittelwerte (%), Standardabweichungen (SD) und maximale Werte (%) für totale Inzuchtkoeffizienten, »neuer« und »alter« Inzucht und partielle Inzuchtkoeffizienten von vier Ahnen für Ferkel, Sauen und Eber bei Edelschwein und Landrasse

	Litter			Dam			Sire		
	mean	SD	max.	mean	SD	max.	mean	SD	max.
<i>Large White</i>									
Total F	2.23	2.26	38.75	2.02	2.33	38.75	1.59	2.21	26.24
Age of F									
F_{new}	1.00	2.36	37.50	0.90	1.99	37.50	0.85	1.86	25.00
F_{old}	1.22	0.65	9.00	1.12	0.96	5.90	0.74	0.89	4.43
Partial F									
A_LW	0.01	0.21	24.59	0.01	0.12	6.68	0.00	0.06	2.82
B_LW	0.12	0.33	12.52	0.10	0.31	12.07	0.05	0.22	3.38
C_LW	0.15	0.34	13.36	0.12	0.33	12.59	0.09	0.33	3.37
D_LW	0.01	0.13	6.31	0.01	0.12	6.51	0.01	0.12	3.13
Rest_LW	1.93	2.39	34.86	1.78	2.13	34.81	1.44	2.02	24.37
<i>Landrace</i>									
Total F	1.24	2.36	31.35	0.93	1.86	26.38	0.67	1.70	25.00
Age of F									
F_{new}	0.89	2.25	31.25	0.67	1.74	35.39	0.53	1.60	25.00
F_{old}	0.34	0.45	4.30	0.26	0.40	3.69	0.14	0.32	2.81
Partial F									
A_LR	0.09	0.47	25.02	0.07	0.44	12.58	0.03	0.23	6.13
B_LR	0.05	0.27	6.60	0.04	0.22	6.39	0.02	0.12	3.32
C_LR	0.11	0.45	12.88	0.07	0.34	11.85	0.05	0.32	6.27
D_LR	0.01	0.22	12.46	0.01	0.18	12.04	0.02	0.19	3.74
Rest_LR	0.97	1.99	31.35	0.74	1.54	25.21	0.56	1.53	25.00

Generally higher litter, dam and sire inbreeding was present in the Large White population. Mean total inbreeding coefficients ranged from 1.59% to 2.23% and from 0.67% to 1.24% for Large White and Landrace, respectively. About 45% to 53% of total inbreeding in Large White and 72% to almost 80% of total inbreeding in Landrace could be traced back to common ancestors in the first five generations (»new« inbreeding). In Large White, the important ancestors A_LW, B_LW, C_LW and D_LW were responsible for 13% of total litter inbreeding, 12% of total dam inbreeding and 9% of total sire inbreeding. In case of Landrace nearly 21% of total litter inbreeding, 20% of total dam inbreeding and 16% of total sire inbreeding was explained by the ancestors A_LR, B_LR, C_LR and D_LR.

Total inbreeding coefficient

Linear regression model

Estimates of the effects of litter, dam and sire inbreeding on total number born, number born alive and weaned piglets in Austrian Large White and Landrace pigs are presented in Table 3. In both populations inbreeding reduced the vitality of the piglets and the mothering abilities of the sow. In Large White dam inbreeding had a significant negative effect on all reproductive traits ($P<0.001$), whereas litter inbreeding showed a significant negative effect on number of piglets born alive ($P<0.01$) and number of piglets weaned ($P<0.001$). A similar pattern was observed for Landrace. In this population a significant negative effect of litter inbreeding on all analysed traits ($P<0.01$ to $P<0.001$) was revealed, whereas dam inbreeding had only a negative effect on number of piglets born alive ($P<0.05$).

Table 3

Effects of litter, dam and sire inbreeding on total number born, number born alive and number weaned per 10% inbreeding in Large White and Landrace

Effekte von Ferkel-, Sau- und Eberinzucht auf die Merkmale gesamt geborene, lebend geborene und hochgezogene Ferkel pro 10% Inzucht für Edelschwein und Landrasse

	Large White		Landrace	
	Regression coefficient	Standard error	Regression coefficient	Standard error
Total number born				
F_l	-0.05	0.04	-0.26**	0.08
F_d	-0.21***	0.05	-0.16	0.10
F_s	-0.02	0.05	0.45**	0.14
Number born alive				
F_l	-0.10**	0.04	-0.25**	0.08
F_d	-0.19***	0.04	-0.12	0.10
F_s	0.03	0.05	0.43***	0.13
Number weaned				
F_l	-0.19***	0.03	-0.29***	0.07
F_d	-0.16***	0.04	-0.21*	0.09
F_s	-0.01	0.05	0.40***	0.12

F_l inbreeding coefficient of litter, F_d inbreeding coefficient of dam, F_s inbreeding coefficient of sire, significant effects $P<0.05$ * $P<0.05$, ** $P<0.01$, *** $P<0.001$

In total -0.19 and -0.29 piglets per 10% increase of litter inbreeding and -0.16 and -0.21 piglets per 10% increase of dam inbreeding were weaned in Large White and Landrace, respectively.

The inbreeding of the sire showed no significant effect on litter traits in Large White. Contrary, sire inbreeding had a significant positive effect on all reproductive traits in Landrace pigs ($P<0.01$ to $P<0.001$). Sires with an inbreeding coefficient of 10% had on average 0.45 more piglets born total and 0.43 more piglets born alive. Subsequently, a positive effect on number of piglets weaned was observed.

Quadratic regression model

In Large White the quadratic regression coefficient was significant for dam inbreeding only (see Table 4). Inbreeding depression of the dam is decreasing slightly with increasing inbreeding. However, the difference between the linear and quadratic regression models

for inbreeding coefficients up to 10% was small. To interpret the results for inbreeding coefficients higher than 10% correctly, it would be necessary to have more animals with inbreeding coefficients higher than 10%. For Landrace no quadratic term turned out to be significant (data not shown). A possible reason is the lower inbreeding level detectable within the Landrace data.

In Large White, inbreeding of the sire showed no significant effect, thus sire inbreeding was excluded in subsequent analyses.

Table 4

Effects of litter, dam and sire inbreeding on total number born, number born alive and number weaned per 10% inbreeding in Large White

Effekte von Ferkel-, Sau- und Eberinzucht auf die Merkmale gesamt geborene, lebend geborene und hochgezogene Ferkel pro 10% Inzucht für Edelschwein

	Regression coefficient	Standard error
Total number born		
F_l	0.00	0.08
$F_l \cdot F_l$	-0.03	0.04
F_d	-0.45***	0.08
$F_d \cdot F_d$	0.17***	0.05
F_s	-0.06	0.09
$F_s \cdot F_s$	0.02	0.07
Number born alive		
F_l	-0.02	0.08
$F_l \cdot F_l$	-0.04	0.04
F_d	-0.40***	0.08
$F_d \cdot F_d$	0.14**	0.05
F_s	-0.04	0.09
$F_s \cdot F_s$	0.05	0.07
Number weaned		
F_l	-0.12	0.07
$F_l \cdot F_l$	-0.03	0.33
F_d	-0.32***	0.07
$F_d \cdot F_d$	0.11**	0.42
F_s	-0.11	0.08
$F_s \cdot F_s$	0.08	0.62

F_l inbreeding coefficient of litter, F_d inbreeding coefficient of dam, F_s inbreeding coefficient of sire, significant effects $P < 0.05$ * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

»New« and »old« inbreeding

The effects of »new« and »old« inbreeding of litter, dam and sire on reproductive performance in Large White and Landrace are shown in Tables 5 to 7.

In both populations the viability of piglets was reduced by »new« and »old« inbreeding. The estimated inbreeding depression was -0.18 and -0.23 piglets weaned per 10% »new« litter inbreeding and -0.31 and -1.91 piglets weaned per 10% »old« litter inbreeding in Large White and Landrace, respectively. Especially in Landrace »old« litter inbreeding had a higher impact on inbreeding depression than »new« inbreeding. In contrast, only »old« inbreeding of dams revealed a significant negative effect on all traits in Large White and Landrace. Furthermore the positive inbreeding effect of sires in the

Landrace population resulted from »new« inbreeding, whereas »old« inbreeding showed a negative effect (not significant) on the traits analysed.

Table 5

»New« and »old« inbreeding effects of litter on total number born, number born alive and number weaned per 10% inbreeding in Large White and Landrace

Effekte von »junger« und »alter« Ferkelinzucht pro 10% Inzucht bei Edelschwein und Landrasse

	Large White		Landrace	
	Regression coefficient	Standard error	Regression coefficient	Standard error
Total number born				
F_{L_new}	-0.07	0.04	-0.22**	0.08
F_{L_old}	0.01	0.13	-1.52**	0.57
F_d	-0.22***	0.05	-0.14	0.10
F_s	—	—	0.51***	0.14
Number born alive				
F_{L_new}	-0.11**	0.04	-0.20*	0.08
F_{L_old}	0.01	0.13	-1.63**	0.55
F_d	-0.20***	0.04	-0.10	0.10
F_s	—	—	0.50***	0.13
Number weaned				
F_{L_new}	-0.18***	0.04	-0.23**	0.07
F_{L_old}	-0.31**	0.12	-1.91***	0.50
F_d	-0.15***	0.04	-0.18*	0.09
F_s	—	—	0.48***	0.12

F_{L_new} new inbreeding of litter, F_{L_old} old inbreeding of litter, F_d inbreeding coefficient of dam, F_s inbreeding coefficient of sire; significant effects $P < 0.05$ * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 6

»New« and »old« inbreeding effects of dam on total number born, number born alive and number weaned per 10% inbreeding in Large White and Landrace

Effekte von »junger« und »alter« Sauenzucht pro 10% Inzucht bei Edelschwein und Landrasse

	Large White		Landrace	
	Regression coefficient	Standard error	Regression coefficient	Standard error
Total number born				
F_l	-0.04	0.04	-0.25**	0.08
F_{d_new}	-0.06	0.05	-0.06	0.11
F_{d_old}	-0.95***	0.13	-2.16***	0.64
F_s	—	—	0.43**	0.14
Number born alive				
F_l	-0.08*	0.04	-0.24**	0.08
F_{d_new}	-0.08	0.05	-0.33	0.10
F_{d_old}	-0.75***	0.12	-1.90**	0.61
F_s	—	—	0.42**	0.13
Number weaned				
F_l	-0.18***	0.03	-0.27***	0.07
F_{d_new}	-0.06	0.05	-0.97	0.09
F_{d_old}	-0.64***	0.11	-2.41***	0.56
F_s	—	—	0.38**	0.12

F_l inbreeding coefficient of litter, F_{d_new} new inbreeding of dam, F_{d_old} old inbreeding of dam F_s inbreeding coefficient of sire, significant effects $P < 0.05$ * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 7

»New« and »old« inbreeding effects of sire on total number born, number born alive and number weaned per 10% inbreeding in Landrace

Effekte von »junger« und »alter« Eberinzucht pro 10% Inzucht bei der Landrasse)

	Regression coefficient	Standard error
Total number born		
F_l	-0.24**	0.08
F_d	-0.17	0.10
F_{s_new}	0.60***	0.15
F_{s_old}	-1.07	0.69
Number born alive		
F_l	-0.23**	0.08
F_d	-0.13	0.10
F_{s_new}	0.56***	0.15
F_{s_old}	-0.85	0.66
Number weaned		
F_l	-0.27***	0.07
F_d	-0.22*	0.09
F_{s_new}	0.52***	0.13
F_{s_old}	-0.72	0.60

F_l inbreeding coefficient of litter, F_d inbreeding coefficient of dam, F_{s_new} new inbreeding of sire, F_{s_old} old inbreeding of sire significant effects $P < 0.05$ * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Partial inbreeding coefficient

An overview of means and standard deviations of inbreeding effects of four genetically important ancestors in Large White and Landrace is given in Figures 1 and 2. A difference in direction and magnitude of inbreeding effects among different ancestors in both populations could be detected. In Large White, the effects of litter and dam inbreeding due to ancestors B_LW and C_LW showed low or no inbreeding depression on all traits. However, the results were not significant. In contrast, dam inbreeding due to sire D_LW revealed a significant negative effect on reproductive performance of the sow. On average, dams with 10% inbreeding due to D_LW had on average 2.0 piglets less born alive.

In Landrace, litter inbreeding due to ancestor C_LR showed a significant negative effect on piglet viability, whereas inbreeding from D_LR reduced the mothering abilities of the sow significantly. Inbred sires in the Austrian Landrace population had on average more piglets born total and born alive. Most interestingly, sire inbreeding due to ancestor

A_LR revealed a significant positive effect on number of piglets born total, whereas sires with 10% inbreeding from C_LR had on average 1.0 less piglets born total and born alive compared to non inbred sires.

Discussion

The mean inbreeding coefficients in this study were low. In comparison, FARKAS *et al.* (2007) reported in their study similar inbreeding coefficients between 0.50% to 0.89% for Hungarian Landrace and Large White pigs. In previous studies from BERESKIN *et al.* (1968) and RODRIGÁÑEZ *et al.* (1998), who analysed experimental pig herds, the observed mean inbreeding was much higher (16.1% to 23.1%).

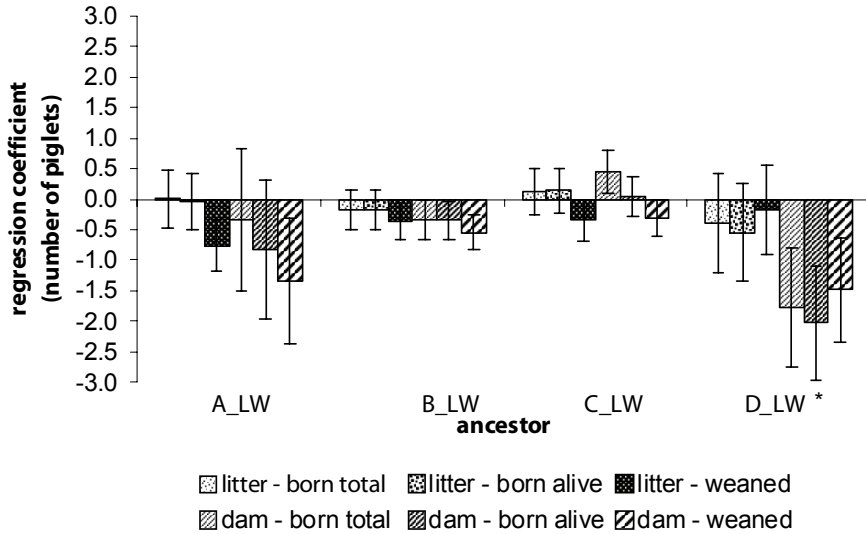


Figure 1
 Partial inbreeding effects (\pm standard error) of litter and dam of four ancestors on total number born, number born alive and number weaned per 10% inbreeding in Large White, significant effects $P < 0.05$: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Partielle Inzuchteffekte (\pm Standardfehler) von Ferkel und Sau auf die Merkmale gesamt geborene, lebend geborene und hochgezogene Ferkel pro 10% Inzucht von vier Ahnen beim Edelschwein, signifikante Effekte $P < 0.05$: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

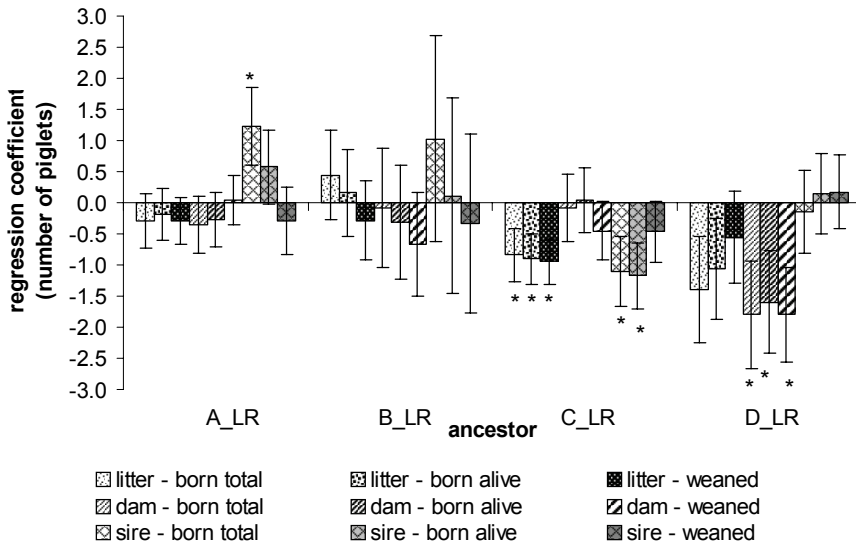


Figure 2
 Partial inbreeding effects (\pm standard error) of litter, dam and sire of four ancestors on total number born, number born alive and number weaned per 10% inbreeding in Landrace, significant effects $P < 0.05$: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Partielle Inzuchteffekte (\pm Standardfehler) von Ferkel, Sau und Eber auf die Merkmale gesamt geborene, lebend geborene und hochgezogene Ferkel pro 10% Inzucht von vier Ahnen bei der Landrasse, signifikante Effekte $P < 0.05$: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

The estimated inbreeding depression due to litter and dam inbreeding coefficients was low in both populations and in agreement with results by BERESKIN *et al.* (1968), RODRIGÁÑEZ *et al.* (1998), CULBERTSON *et al.* (1998) and FARKAS *et al.* (2007). The inbreeding of the sire showed no significant effect on litter traits in Large White. BERESKIN *et al.* (1968) also detected no significant influence of sire inbreeding on litter size. In contrast to these results, a positive sire inbreeding effect on all litter traits was observed in the Landrace population. The positive inbreeding effect is most likely caused by a better sperm quality of the inbred sires. Generally positive inbreeding effects on fitness and fertility traits are rare. SHIELDS (1982) originally called such a phenomenon »inbreeding enhancement«. LACY *et al.* (1996) and MARGULIS (1998) found a positive effect of dam inbreeding on offspring viability in a subspecies of the old-field mouse, *Peromyscus polionotus*. Furthermore BALLOU (1997) observed a significant positive effect of maternal inbreeding on neonatal survival in European bison. The increase in fitness is probably due to fixation of favourable gene complexes or epistatic relationships (TEMPELTON 1979). On the other hand, outcrossing does not always enhance fitness. Crosses between distant populations of the same species sometimes lead to significant outbreeding depression. The decline in reproductive fitness under outcrossing is usually attributed to a break up of coadapted gene complexes or favourable epistatic relationships (genetic incompatibility) (FALCONER & MACKAY 1996, EDMANDS 2007, RALLS *et al.* 2007). Like crossbreeding has not always beneficial effects on fitness, inbreeding is not always detrimental.

Non-linear inbreeding effects on reproductive performance were only observed for dam inbreeding in Large White. BERESKIN *et al.* (1968) also revealed non-linear effects of inbreeding on litter size in pigs. In recent studies with mice (ISSA & SEELAND 2001), poultry (SZWACZKOWSKI *et al.* 2004) and cattle (CROQUET *et al.* 2007) non-linear inbreeding effects on production and fitness traits were detected. Generally, the differences between linear and curvilinear regression models are very small between 0 and 10% of inbreeding.

The observed inbreeding effects in Large White and Landrace were not only caused by recent inbreeding. Fertility is also affected by old inbreeding. In Landrace, the positive effect of sire inbreeding was caused by recent inbreeding from the first five generations. This result gives further evidence that epistatic interactions may be responsible for the positive inbreeding effect. »Old« inbreeding showed a negative effect (not significant) on the analysed traits, mating with more distant relatives may have broken up these positive interactions. In a long-term selection experiment on first-litter size in mice HINRICHS *et al.* (2007) also investigated differences between the effects of inbreeding in recent generations from that in the past. The analysis was repeated for different definitions of »new« and »old« inbreeding, depending on length of the »new« period. In this mouse population the »new« inbreeding was found to cause more inbreeding depression than the »old« inbreeding when at least 25 generations were classified as »new« inbreeding.

Overall inbreeding had small effects on reproductive performance in Large White and Landrace pigs. However, some differences in direction and magnitude of inbreeding effects among different ancestors were detected. Alleles contributing to inbreeding depression were descendent from specific ancestors. Variable effects of inbreeding were already reported. PRAY and GOODNIGHT (1995) revealed that inbreeding effects vary for fitness traits among lineages in the red flour beetle. LACY *et al.* (1996) detected

heterogeneity in inbreeding effects for survival, reproduction and growth traits among different founder pairs in the old-field mouse. Also, RODRIGÁÑEZ *et al.* (1998) found heterogeneous effects of inbreeding on litter size in five founder lineages of Large White pigs. Recent studies in dairy cattle detected variation of inbreeding effects for production traits in different families in Canadian Holstein cows (MIGLIOR *et al.* 1994) and US Jersey cows (GULISIJA *et al.* 2006). The differences among founders and lineages in inbreeding depression indicate that relatively few deleterious alleles with major effects contribute to inbreeding depression for any one trait. This finding is especially important for endangered species and breeds, where the inbreeding level is much higher. For example, Maignel and Labroue (2001) and KOLK GEN SUNDAG *et al.* (2006) reported for endangered pig breeds average inbreeding coefficients between 8 and 18%. Thus the main aim in conservation programmes is to minimize inbreeding depression. In the future may be greater emphasis could be given to the partial inbreeding components.

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References

- Ballou JD (1997) Ancestral inbreeding only minimally affects inbreeding depression in mammalian populations. *J Hered* 88, 169-78
- Baumung R, Suwanlee S, Boichard D, Sölkner J, Curik I (2006) GRain: A Computer Program for Calculation of various Ancestral and Partial Inbreeding Coefficients from Pedigree Records. In: Suwanlee S, Ancestral inbreeding. PhD Thesis, University of Natural Resources and Applied Life Sciences, Vienna, Austria
- Bereskin B, Shelby CE, Rowe KE, Urban Jr WE, Blunn, CT, Chapman AB, Garwood VA, Hazel LN, Lasley JF, Magee WT, Mccarty JW, Whatley Jr A (1968) Inbreeding and Swine Productivity Traits. *J Anim Sci* 27, 339-50
- Boichard D, Maignel L, Verrier É (1997) The value of using probabilities of gene origin to measure genetic variability in a population. *Genet Sel Evol* 29, 5-23
- Boichard D (2002) PEDIG: a fortran package for pedigree analysis suited for large populations. 7th World Congress on Genetics Applied to Livestock Production, Montpellier, 19-23 août 2002, paper 28-13
- Boichard D (2007) PEDIG: a fortran package for pedigree analysis suited for large populations. Updated August 2007. http://www-sgqa.jouy.inra.fr/IMG/pdf/User_s_Guide.pdf [last accessed 18.06.2008]
- Croquet C, Mayeres P, Gillon A, Hammami H, Soyeurt H, Vanderick S, Gengler N (2007) Linear and Curvilinear Effects of Inbreeding on Production Traits for Walloon Holstein Cows. *J Dairy Sci* 90, 465-71
- Crow JF (1952) Dominance and overdominance, in Gowen JW (Ed) *Heterosis*. Iowa State College Press, Ames, IA, USA, 282-94
- Culbertson MS, Mabry JW, Misztal I, Gengler N, Bertrand JK, Varona I (1998) Estimation of Dominance Variance in Purebred Yorkshire Swine. *J Anim Sci* 76, 448-51
- Darwin CR (1876) *The effects of cross and self-fertilization in the vegetable kingdom*. Murray, London, UK
- Davenport CB (1908) Degeneration, albinism and inbreeding. *Sci* 28, 454-5
- De Rose MA, Roff DA (1999) A comparison of inbreeding depression in life-history and morphological traits in animals. *Evol* 53, 1288-92
- East EM (1908) Inbreeding in corn. Reports of the Connecticut Agricultural Experiments Station for 1907, 419-29
- Edmands S (2007) Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management. *Mol Ecol* 16, 463-75
- Falconer DS, Mackay TFC (1996) *Introduction to quantitative genetics*, 4th ed Longman, Harlow, UK

- Farkas J, Curik I, Csató L, Csörnyei Z, Baumung R, Nagy I (2007) Bayesian inference of inbreeding effects on litter size and gestation length in Hungarian Landrace and Hungarian Large White pigs. *Livest Sci* 112, 109-14
- Frankham R, Ballou JD, Briscoe DA (2002) *Introduction to Conservation Genetics*. Cambridge University Press, Cambridge, UK
- Gulisija D, Gianola D, Weigel KA, Toro MA (2006): Between-founder heterogeneity in inbreeding depression for production in Jersey cows. *Livest Sci* 104, 244-53
- Hedrick PW, Kalinowski ST (2000) Inbreeding depression in conservation biology. *Ann Rev Ecol Syst* 31, 523-37
- Hinrichs D, Meuwissen THE, Ødegard J, Holt M, Vangen O, Woolliams JA (2007) Analysis of inbreeding depression in the first litter size of mice in a long-term selection experiment with respect to the age of the inbreeding. *Heredity* 99, 81-8
- Issa BS, Seeland G (2001) Effect of inbreeding and selection on fertility and growth in mice. *Arch Tierz* 44, 671-6 [in German]
- Keller LF, Waller DM (2002) Inbreeding effects in wild populations. *Tren Ecol Evol* 17, 230-41
- Kolk Gen Sundag C, Wrede J, Distl O (2006) Analysis of the population structure of the Black and White Bentheim pig. *Arch Tierz* 49, 447-61 [in German]
- Lacy RC, Alaks G, Walsh A (1996) Hierarchical analysis of inbreeding depression in *Peromyscus polionotus*. *Evolution* 50, 2187-200
- Maignel L, Labroue F (2001) Study of the genetic variability of selected and local breeds using pedigree information. *J Rech Porc France* 33, 111-17 [in French]
- Malécot G (1948) *The mathematics of heredity*. Masson et Cie, Paris, France [in French]
- Margulis SW (1998) Relationship among parental inbreeding parental behaviour and offspring viability in oldfield mice. *Anim Behav* 55, 427-38
- Miglior F, Burnside EB, Hohenboken WD (1994) Heterogeneity among families of Holstein cattle in inbreeding depression for production traits. *Proceedings of the 5th World Congress Genetics Applied Livestock Production* 18, 479-82
- Pray LA, Goodnight CJ (1995) Genetic variation in inbreeding depression in the red flour beetle *Tribolium Castaneum*. *Evolution* 49, 176-88
- Ralls K, Frankham R, Ballou JD (2007) Inbreeding and outbreeding. In: Levin SA (Ed) *Encyclopedia of Biodiversity Vol 3*, Academic press San Diego CA, 427-35
- Rodríguez J, Toro MA, Rodríguez MC, Silió L (1998) Effect of founder allele survival and inbreeding depression on litter size in a closed line of Large White pigs. *Anim Sci* 67, 573-82
- SAS (2003) SAS Version 9.1 SAS Institute Inc., Cary NC, USA
- Shields WM (1982) *Philopatry inbreeding and the evolution of sex*. State University of New York Press, Albany, New York, USA
- Shull GH (1908) The composition of a field of maize. *Ann Breed Assoc* 4, 296-301
- Szwaczkowski T, Cywa-Benko K, Wężyk S (2004) Curvilinear inbreeding effects on some performance traits in laying hens. *J Appl Genet* 45, 343-5
- Templeton AR (1979) The unit of selection in *Drosophila Mercatorum*. II. Genetic revolution and the origin of coadapted genomes in parthenogenetic strains. *Genetics* 92, 1265-82
- Templeton AR, Read B (1994) Inbreeding one word several meanings much confusion. In: Loeschke V, Tomiuk J, Jain SK (Eds) *Conservation genetics*. Birkhäuser, Basel, Swiss, 91-105
- Thornhill NW (1993) *Natural history of inbreeding and outbreeding. Theoretical and empirical perspectives*. University of Chicago Press, Chicago, USA
- Van Raden PM (1992) Accounting for inbreeding and crossbreeding in genetic evaluation of large population. *J Dairy Sci* 75, 3136-44
- Wright S (1922) Inbreeding coefficients and relationship. *Amer Nat* 56, 330-8

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Corresponding author:

PD Dr. ROSWITHA BAUMUNG

email: roswitha.baumung@boku.ac.at

Division of Livestock Sciences, University of Natural Resources and Applied Life Sciences Vienna, Gregor Mendel-Str. 33, 1180 Vienna, Austria
