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Consequences of long-term inbreeding accumulation on preweaning traits in a closed nucleus Angus herd

J. A. Carrillo and F. Siewerdt

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ABSTRACT: The effect of individual and dam (maternal) inbreeding was quantified for preweaning traits in an Angus nucleus herd that has been closed to outside breeding for 70 yr. The effectiveness of 5 models (linear, quadratic, exponential, Michaelis-Menten, and Rumford-Newton) was evaluated for describing the effect of inbreeding on growth traits, hock length (HL), and scrotal circumference (SC). Pedigree information and production records were retrieved for 10,938 animals and analyzed in an animal model that included the fixed effects of year of birth, age of the dam, sex, and age at weaning (for traits measured at weaning). Average individual and maternal inbreeding in the herd were 0.068 and 0.066, respectively, for all animals; in the last calf crop these values were 0.120 for the calves and 0.121 for their dams. Inbreeding depression was observed for BW at birth (WB), weaning weight (WW), BW adjusted to 205 d of age (W205), ADG, HL, and SC. The effect of maternal inbreeding was smaller than for individual inbreeding for WB, WW, W205, and ADG. Nonlinear prediction was done more effectively by the exponential and Michaelis-Menten models. Quadratic polynomials were an inadequate descriptor of inbreeding effects. Genetic gain from selection at an intensity equivalent to 0.25 can be nullified by an inbreeding accumulation of 0.187 (WB), 0.056 (WW), 0.068 (W205), 0.065 (ADG), or 0.092 (SC). Inbreeding accumulation of 0.018 is required to nullify genetic gain for HL; this particular prediction is valid for non-inbred cows due to an observed interaction between individual and maternal inbreeding. At current inbreeding accumulation levels in this herd, 7 generations of inbreeding accumulation will be necessary to nullify the genetic progress from 1 generation of selection in growth traits.

Key words: beef cattle, growth, inbreeding depression, nucleus herd, scrotal circumference

INTRODUCTION

Inbreeding is the consequence of mating related individuals. In diploid species, inbred individuals will carry 2 copies of the same allele that are identical by descent (i.e., from a common ancestor), through DNA replication (Malécot, 1969). Genetic management of livestock should contemplate not reaching levels of inbreeding in future generations where it would be possible to observe a reduction in biological performance or a threat to the sustainability of selection programs. Reproduction and fitness traits are usually more sensitive to inbreeding accumulation than growth and morphological traits (McParland et al., 2007). Inbreeding depression is expected at reduced levels of inbreeding in fitness traits than in traits that measure growth, carcass composition and quality, or feed utilization.

Cleveland et al. (2005) reported that the annual rate of inbreeding accumulation in the entire US Hereford breed from 1990 to 2001 was estimated to be 0.12%. Cleveland et al. (2005) estimated the effective population size of the US herd at 85, which is a marginal size for avoiding severe declines in fitness (Meuwissen and Wooliams, 1994). The effects of direct and maternal inbreeding on preweaning traits in beef cattle are well documented. Conflicting reports can be found on the influence of maternal inbreeding on birth weight and other traits (MacNeil et al., 1989; Snelling et al., 1996; Pariacone et al., 1998; Casas et al., 2007; Carolino and Gama, 2008). Pariacone et al. (1998) have suggested that an interaction between the effects of direct and maternal inbreeding may be the source of some inconsistencies.

The objective of this study was to determine the effects of direct and maternal inbreeding accumulation and their interaction on preweaning traits measured in calves from a closed nucleus Angus herd and to establish the critical levels where inbreeding depression...
Table 1. Population descriptors for the 6 preweaning traits

<table>
<thead>
<tr>
<th>Trait</th>
<th>n</th>
<th>Mean</th>
<th>SD</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birth weight, kg</td>
<td>8,002</td>
<td>33.7</td>
<td>4.5</td>
<td>13.6</td>
<td>56.7</td>
</tr>
<tr>
<td>Weaning weight, kg</td>
<td>8,005</td>
<td>232.4</td>
<td>37.0</td>
<td>74.4</td>
<td>396.9</td>
</tr>
<tr>
<td>Adjusted weight, 205 d, kg</td>
<td>8,004</td>
<td>232.0</td>
<td>29.0</td>
<td>80.3</td>
<td>333.9</td>
</tr>
<tr>
<td>ADG, kg</td>
<td>8,002</td>
<td>0.921</td>
<td>0.138</td>
<td>0.245</td>
<td>1.470</td>
</tr>
<tr>
<td>Hock length, cm</td>
<td>3,295</td>
<td>26.6</td>
<td>1.11</td>
<td>21.6</td>
<td>30.5</td>
</tr>
<tr>
<td>Scrotal circumference, cm</td>
<td>1,857</td>
<td>21.6</td>
<td>3.1</td>
<td>14.0</td>
<td>41.0</td>
</tr>
</tbody>
</table>

Materials and Methods

No animal care and use protocol was required by the host institution because this work was conducted with existing pedigree information and farm production records. Data were obtained from the records of the Wye Research and Education Center, University of Maryland, who is the current owner of the herd.

The Wye Angus herd was established in 1937 with the acquisition of the first 2 bulls and 18 yearling heifers (Lingle et al., 2001). Ten of those heifers were paternal half-sisters; 2 other clusters of paternal half-sisters included 4 and 2 of those heifers. No further known genetic ties existed between the 3 groups and the remaining 2 heifers (Brinks and Katsigianis, 1982). In 1939, 8 additional heifers from a different source were added to the herd (a group of 4 and another group of 2 were paternal half-sisters). One of the founder bulls had 2.3% inbreeding and an average 2.1% relationship to the 18 founding heifers. The second founder bull had a greater inbreeding level (15.7%) and was related to the first bull (5.3%) but only slightly related to the founder heifers (0.2%). Nineteen bulls of imported ancestry were added to the herd during the next 2 decades. These bulls had average inbreeding of 2.7% but were unrelated to the foundation animals. Seven pairs of those bulls were paternal half-sibs and the majority of the other bulls had less than 6% relationship among them (Brinks and Katsigianis, 1982). The first calf crop was in 1939. The herd was closed to outside breeding after the introduction of the last bulls and has remained a close herd ever since. This special condition of the Wye Angus herd makes it a distinctive resource for studying long-term effects of inbreeding accumulation in a moderate-sized closed herd.

Husbandry systems have changed since the inception of this herd. From 1988 there has been a single yearly crop in the winter. Animals are raised in a semi-intensive system, kept in grazing paddocks, and supplemented with hay as needed. Forages are mainly composed of clover and fescue but alfalfa and orchard grass are also grown for hay production. Artificial insemination started being used early in the 1960s decade, but only semen from bulls of this herd was used. At present, it is used as the preferred form of reproduction; females that do not become pregnant receive a second opportunity in the mating season by being placed in a paddock with a single service bull. Approximately 170 cows and replacement heifers are bred each year. In their first year, replacement females receive corn silage for a target daily BW gain of 0.8 to 0.9 kg. Hay supplement is offered to these heifers in their second and third years. After producing their second calf, they join the older cows in the pasture and hay supplement regimen.

Body weights are recorded at birth within the first 24 h (WB) and at weaning (WW). Weaning weights were adjusted to a constant 205-d basis (W205) by employing an additive correction factor generated specifically for this herd. The ADG from birth to 205 d was obtained for every weaned calf. Hock length (HL) was measured at birth. Scrotal circumference (SC) was measured at weaning. Descriptive statistics on the 6 traits are shown in Table 1.

The pedigree had N = 10,938 animals including the founder animals and several of their ancestors. Parental information on the founder and imported animals was extended through at least 4 generations by searching the records of the American Angus Association Herd Book. Pedigree information was available for the founder animals and their ancestors, but data collection spanned the last 53 yr, from the calf crop of 1954 to 2006.

A single-trait animal model was used to analyze the data. The model included the fixed effects of year of birth and age of the dam, the latter as a covariable. Age at weaning was used as a linear covariable for WW, ADG, and SC. Sex was included as a fixed effect on those traits measured on males and females. Random effects in the model were the direct genetic, maternal genetic, and permanent environment (dam):

\[ y = X\beta + Z_1a + Z_2m + Z_3c + e, \]

where \( y \) is a vector with the phenotypic observations on a trait, \( \beta \) is a vector of fixed effects, \( a \) is a vector with breeding values for direct genetic effects, \( m \) is a vector with breeding values for maternal genetic effects, \( c \) is a vector with permanent environmental effects associated to each dam, \( e \) is a vector with the random errors, and \( X, Z_1, Z_2, \text{ and } Z_3 \) are design and incidence matrices that relate each observation to the corresponding levels and values of its fixed and random effects. Random errors were assumed to be independent and to have normal distribution \((0, \sigma^2_e)\).
The expected values of all vectors are 
\[ E[y \ a \ m \ c \ e] = [X\beta \ \bar{a} \ m \ 0 \ 0]. \]

The expectation 
\[ E[a \ m] = [0 \ 0] \]
holds true for animals at the base generation, assuming absence of selection leading to this generation (Henderson, 1984). The assumed covariance structure is

\[
V = \begin{bmatrix}
A\sigma^2_a & A\sigma_{am} & 0 & 0 \\
A\sigma_{am} & A\sigma^2_m & 0 & 0 \\
0 & 0 & I_n\sigma^2_c & 0 \\
0 & 0 & 0 & I_n\sigma^2_e
\end{bmatrix},
\]

where \( V \) are variances, \( A \) is the additive genetic relationship matrix, \( I \) is the identity matrix, and \( n \) is the number of cows with at least one calf.

Statistical analyses were done with the software MTDFFREML (Boldman et al., 1995). Inbreeding coefficients were obtained for each animal with the first module of the software (MTDFNRM, Boldman et al., 1995). It was also assumed that records on all calves were affected by inbreeding (maternal inbreeding) of their dams. The effect of inbreeding on the traits was determined by fitting several regression models to the errors generated by the animal model. The general form of these supplementary analyses was \( e_i = \Phi(F_i) + \epsilon_i \), where \( \epsilon_i \) are the estimated errors in the vector \( e = y - X\beta - Z_a\sigma - Z_m m - Z_c c \). \( \Phi(F_i) \) is a given regression function on the inbreeding coefficient of the animal \( (F_i) \) or of the dam \( (F_m) \), and \( \epsilon_i \) are the deviations of the errors from the predicted ones in the regression function. It was assumed that no interaction was present between the effects of inbreeding and the fixed effects (Burrow, 1998), breeding values, or environmental effects. This 2-step analysis was necessary because MTDFFREML limits the possible concomitant regression analysis (as covariables) to polynomial models.

The regression models studied were linear, quadratic, exponential, and Rumford-Newton.

\[
e_i = \beta_0 + \beta_1(F_i - \bar{F}) + \epsilon_i; \quad \text{linear,}
\]

\[
e_i = \beta_0 + \beta_1(F_i - \bar{F}) + \beta_2(F_i - \bar{F})^2 + \epsilon_i; \quad \text{quadratic,}
\]

\[
e_i = \alpha \beta^{\theta_i} + \epsilon_i; \quad \text{exponential,}
\]

\[
e_i = \alpha + \beta \exp(-\theta F_i) + \epsilon_i; \quad \text{Rumford-Newton.}
\]

Coefﬁcients of determination were compared as measures of goodness of fit. Hypothesis tests were conducted for the critical parameters of each regression model, namely \( H_0: \beta_1 = 0 \) (linear), \( H_0: \beta_2 = 0 \) (quadratic), \( H_0: \beta = 1 \) (exponential), \( H_0: \beta_2 = 0 \) (Michaelis-Menten), and \( H_0: \theta = 0 \) (Rumford-Newton). Degrees of freedom for these hypothesis tests were adjusted by subtracting the degrees of freedom for fixed effects in the first step of the analysis. The interaction between the effects of individual and maternal inbreeding was also examined; this interaction was limited to a linear by linear format:

\[
e_i = \beta_0 + \beta_1(F_i - \bar{F}) + \beta_2(F_m - \bar{F}) + \beta_1\beta_2(F_i - \bar{F})(F_m - \bar{F}) + \epsilon_i.
\]

Losses due to inbreeding accumulation that nullify 1 generation of genetic progress due to weak selection were determined for each trait. Weak selection was deﬁned by setting the selection intensity at \( i = 0.25 \), to emulate a situation where the trait in question is part of a broader selection index with multiple traits. The exponential model was used to predict the genetic gains, using the genetic parameters estimated by F. Siewerdt, J. A. Carrillo, and E. C. Draper (Wye Research and Education Center, Queenstown, MD; unpublished data). Because the exponential model predicts a decrease due to inbreeding depression that is not linear, inbreeding depression was estimated for a starting inbreeding value of zero; the base phenotypic value was the estimated intercept of the model. Standard errors for the required inbreeding accumulation were obtained by using a first-order Taylor series approximation for the variance of the ratio of the predicted genetic gain (\( \Delta G \)) and the regression coefﬁcient (\( \beta \)) of the exponential prediction model. For HL the linear regression coefﬁcient (\( \beta_1 \)) was substituted. It was further assumed that the \( \text{Cov}(\Delta G, \beta) = 0 \), or \( \text{Cov}(\Delta G, \beta_1) = 0 \), for HL.

**RESULTS**

Age of dams at calving ranged from 2 to 20 yr with an average age of 5.27 yr. Cows aged 7 yr or younger produced 78.4% of the calves; 2-yr-olds produced 21.6% of the births. Inbreeding values ranged from 0 to 0.422 in the herd. The average inbreeding was 0.075 on 8,582 animals, leaving 21.5% of all animals in the pedigree assumed to have no inbreeding. The proportions of inbred calves and the inbreeding of their dams in each calf crop year are presented in Figure 1. The last non-inbred calf was born in 1998, whereas the last year in which a non-inbred dam gave birth to a calf was in 2002. The average inbreeding on the 2006 calf crop was 0.120, ranging from 0.063 to 0.229, whereas the maternal inbreeding on these calves averaged 0.121, ranging from 0.063 to 0.222. Maternal inbreeding in the entire herd averaged 0.066, ranging from 0 to 0.375. Among the animals with a record, the greatest individual inbreeding values were of 0.385 for all traits except HL (0.327) and SC (0.325). Likewise, the maximum values of maternal inbreeding for animals with a record were 0.296 (WB), 0.375 (WW, W205, and ADG), and 0.278 (HL and SC). Figure 2 shows the historical change of the average individual and maternal inbreeding in the herd. A spike in inbreeding occurred within the first 12 yr of the herd because of its small effective population size. After the additional 19 bulls were incorporated into the breeding herd, average herd inbreeding in sub-
sequent calf crops dropped to near-zero values before a steady annual increase of approximately 0.35% followed for the next 30 yr. By 1990 one historical sire was genetically overrepresented in the population. A breeding management decision was made to shift the emphasis of representation to 3 other sires to reduce the average inbreeding of recruits, which had averaged 0.125 in the previous 4 calf crops. Maternal inbreeding accumulation followed the same trend with a lag of about 5 yr.

The distribution of individual and maternal inbreeding values across the entire herd is presented in Figure 3. It can be noted that 53.5% of the calves and 50.5% of the dams had inbreeding levels between 0.05 and 0.15 and between 0.025 and 0.125, respectively. Less than 1% of the calves had inbreeding of 0.30 or greater; only 8 dams fell in that same group.

A comparison of the different models used to evaluate the direct and maternal inbreeding effects is presented in Table 2. The coefficients of determination of the models, for all traits, were very small. The linear, exponential, and Michaelis-Menten models were the most adequate and were similarly efficient predictors of

[Graphs and figures are not transcribed here.]

Figure 1. Percentage of inbred calves and inbred cows by calf crop year.

Figure 2. Average yearly values of individual and maternal inbreeding.
all traits. Only one Rumford-Newton model was significant, when using individual inbreeding for predicting WW, \( y = 237.9 - 2.927 \text{exp}(5.316F_x) \). In general, this model had computational problems that resulted in a singular Hessian matrix, which can be interpreted as the model not being adequate for describing the biology of inbreeding effects. Fitting a quadratic model to the data was not consistently successful.

Inbreeding accumulation generally caused a reduction in all traits except SC and HL (Table 3). Only the exponential model detected an influence of inbreeding on SC \( (P = 0.049) \). Similarly, maternal inbreeding resulted in a reduction of values of the same traits mentioned above and SC. The effect of maternal inbreeding was smaller than the one of individual inbreeding for WB, WW, W205, and ADG. The exponential and Michaelis-Menten models predicted a reduction in values for the traits that accelerate as inbreeding accumulates.

The interaction between individual and maternal inbreeding was only influential for HL \( (P = 0.015; \text{Figure } 4) \). Prediction of HL with the fitted equation

\[
\hat{y} = 27.453 - 6.122F_x - 2.768F_m - 28.414(F_x \times F_m)
\]

Table 2. Comparison of the 5 regression models as descriptors of the effect of individual and maternal inbreeding on preweaning traits

<table>
<thead>
<tr>
<th>Trait</th>
<th>Inbreeding type</th>
<th>Linear</th>
<th>Quadratic</th>
<th>Exponential</th>
<th>Michaelis-Menten</th>
<th>Rumford-Newton</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birth weight</td>
<td>Individual</td>
<td>0.21**</td>
<td>0.22</td>
<td>0.21**</td>
<td>0.21**</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>Maternal</td>
<td>0.19**</td>
<td>0.25*</td>
<td>0.19**</td>
<td>0.17**</td>
<td>0.17</td>
</tr>
<tr>
<td>Weaning weight</td>
<td>Individual</td>
<td>0.68**</td>
<td>0.78**</td>
<td>0.68**</td>
<td>0.71**</td>
<td>0.74*</td>
</tr>
<tr>
<td></td>
<td>Maternal</td>
<td>0.26**</td>
<td>0.26</td>
<td>0.26**</td>
<td>0.26**</td>
<td>0.26*</td>
</tr>
<tr>
<td>Adjusted BW, 205 d</td>
<td>Individual</td>
<td>0.94**</td>
<td>0.99</td>
<td>0.94**</td>
<td>0.97**</td>
<td>0.97</td>
</tr>
<tr>
<td></td>
<td>Maternal</td>
<td>0.25**</td>
<td>0.41**</td>
<td>0.35**</td>
<td>0.32**</td>
<td>0.41</td>
</tr>
<tr>
<td>ADG</td>
<td>Individual</td>
<td>0.75**</td>
<td>0.84**</td>
<td>0.75**</td>
<td>0.78**</td>
<td>0.75*</td>
</tr>
<tr>
<td></td>
<td>Maternal</td>
<td>0.25**</td>
<td>0.25</td>
<td>0.25**</td>
<td>0.25**</td>
<td>0.25*</td>
</tr>
<tr>
<td>Hock length</td>
<td>Individual</td>
<td>0.01</td>
<td>0.16</td>
<td>0.01</td>
<td>0.02</td>
<td>0.01*</td>
</tr>
<tr>
<td></td>
<td>Maternal</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00*</td>
</tr>
<tr>
<td>Scrotal circumference</td>
<td>Individual</td>
<td>0.20</td>
<td>0.25</td>
<td>0.19*</td>
<td>0.21</td>
<td>0.20*</td>
</tr>
<tr>
<td></td>
<td>Maternal</td>
<td>0.39**</td>
<td>0.39</td>
<td>0.39**</td>
<td>0.38*</td>
<td>0.39*</td>
</tr>
</tbody>
</table>

Table values are 100 × \( r^2 \). Significance levels refer to the hypothesis test of the critical parameter of each regression model.

* \( P < 0.05 \), ** \( P < 0.01 \).

Results may be spurious because the Hessian was singular.

![Figure 3](image1.png)

Figure 3. Distribution of the values of individual and maternal inbreeding in the herd.
had $r^2 = 0.022$, which was the greatest $r^2$ value in this study. Marginal regressions for either measure of inbreeding were not statistically significant for HL.

Levels of inbreeding accumulation required to cancel out one generation of genetic progress accrued by weak selection pressure are shown in Table 4. Calf WB requires the greatest inbreeding accumulation to nullify genetic gains from selection. Growth traits (WW, W205, and ADG) require a smaller inbreeding accumulation (around 6%) for inbreeding depression to become detrimental. For SC an unfavorable reduction in phenotypic values due to accumulation of inbreeding had an intermediate value. Similar inferences for HL must take into account simultaneously the individual and maternal inbreeding due to the interaction. The table value presented is valid for the particular case when there is no maternal inbreeding; thus, its interpretation is not made as a marginal result for individual inbreeding over all possible values of maternal inbreeding. The necessary inbreeding accumulation in HL when $F_m = 0$ to nullify the genetic gain in one generation is the least among all traits. For non-inbred cows, an accumulation of 0.018 is required, which translates to only 2 generations of inbreeding accumulation with the current effective population size in the Wye herd.

### DISCUSSION

Modern tools used in selection programs have contributed to a steady increase in inbreeding levels in almost every livestock species. Biological improvement in reproduction technology (e.g., AI, multiple ovulation and embryo transfer, in vitro fertilization, cloning) allow for greater contribution of fewer breeding individuals to later generations. The same is attainable with advanced statistical methods that rely on selection indexes with family information (e.g., BLUP, Henderson, 1984); indiscriminate selection based strictly on predicted breeding values without acknowledging the need for proper family representation can result in reduction of the gene pool, compromising long-term accrual of selection gains.

Inbreeding depression can be quantified as the reduction of the mean phenotypic value of a trait, mostly related to reproductive capacity or physiological efficiency (Falconer and Mackay, 1996), although it can be also observed for growth and feed utilization traits. Inbreeding depression is a combination of 2 causes at the locus level. The first cause is the reduction of the amount of heterozygosity, which directly affects the ability for exploiting direct dominance genetic effects. The second cause is the negative consequence of homozygosity in some loci; the lack of 1 allele could have unfavorable consequences if that allele codes for an enzyme that is a critical player in a biochemical pathway that affects the phenotype being measured. It is likely that the former cause is usually more important due to the accumulation of several small losses that have

<table>
<thead>
<tr>
<th>Trait</th>
<th>Inbreeding type</th>
<th>Model</th>
<th>Linear</th>
<th>Quadratic</th>
<th>Exponential</th>
<th>Michaelis-Menten</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birth weight</td>
<td>Individual</td>
<td>Linear</td>
<td>β = 2.10 ± 0.54</td>
<td>β = 1.39 ± 0.23</td>
<td>β = 3.55 ± 0.60</td>
<td>β = 0.437 ± 0.015</td>
</tr>
<tr>
<td></td>
<td>Maternal</td>
<td>Linear</td>
<td>β = 0.126 ± 0.05</td>
<td>β = 0.014 ± 0.03</td>
<td>β = 0.065 ± 0.03</td>
<td>β = 0.065 ± 0.03</td>
</tr>
<tr>
<td>Weaning weight</td>
<td>Individual</td>
<td>Linear</td>
<td>β = 4.02 ± 0.82</td>
<td>β = 1.20 ± 0.10</td>
<td>β = 1.80 ± 0.46</td>
<td>β = 0.944 ± 0.015</td>
</tr>
<tr>
<td></td>
<td>Maternal</td>
<td>Linear</td>
<td>β = 2.47 ± 0.63</td>
<td>β = 0.181 ± 0.05</td>
<td>β = 0.055 ± 0.13</td>
<td>β = 0.055 ± 0.13</td>
</tr>
<tr>
<td>Adjusted BW-205 d</td>
<td>Individual</td>
<td>Linear</td>
<td>β = 25.76 ± 3.49</td>
<td>β = 15.68 ± 6.07</td>
<td>β = 77.32 ± 3.49</td>
<td>β = 0.937 ± 0.015</td>
</tr>
<tr>
<td></td>
<td>Maternal</td>
<td>Linear</td>
<td>β = 14.64 ± 3.21</td>
<td>β = 15.68 ± 6.07</td>
<td>β = 77.32 ± 3.49</td>
<td>β = 0.937 ± 0.015</td>
</tr>
<tr>
<td>ADG</td>
<td>Individual</td>
<td>Linear</td>
<td>β = 0.110 ± 0.014</td>
<td>β = 0.008 ± 0.003</td>
<td>β = 0.051 ± 0.013</td>
<td>β = 0.051 ± 0.013</td>
</tr>
<tr>
<td></td>
<td>Maternal</td>
<td>Linear</td>
<td>β = 0.058 ± 0.013</td>
<td>β = 0.055 ± 0.03</td>
<td>β = 0.055 ± 0.03</td>
<td>β = 0.055 ± 0.03</td>
</tr>
<tr>
<td>Scrotal circumference</td>
<td>Individual</td>
<td>Linear</td>
<td>β = 2.29 ± 0.35</td>
<td>β = 1.39 ± 0.23</td>
<td>β = 3.55 ± 0.60</td>
<td>β = 0.437 ± 0.015</td>
</tr>
<tr>
<td></td>
<td>Maternal</td>
<td>Linear</td>
<td>β = 14.13 ± 2.67</td>
<td>β = 15.68 ± 6.07</td>
<td>β = 77.32 ± 3.49</td>
<td>β = 0.937 ± 0.015</td>
</tr>
</tbody>
</table>

1 The significance of the estimators in the exponential model was tested under $H_0: \beta = 1$. Estimates are not presented when the critical parameter was not statistically significant.
an immediate impact on the phenotype due to lack of heterozygosity. The latter cause will have an immediate impact if present through lethality or complete suppression of reproduction or if it is only expressed in greater levels of inbreeding, as a sum of cumulative effects expressed as epistatic interactions; thus, it can be expected that these effects should be less frequent at decreased inbreeding levels. Li et al. (2001) suggested that complex epistatic overdominance effects may be lost due to inbreeding depression, more as a loss in exploitation of heterosis than the expression of alleles that are unfavorable to fitness or production.

Inbreeding levels in the Wye Angus herd are still relatively low. The inbreeding figures in the 2006 calf crop are a result of purposeful avoidance of breeding of closely related animals. From calf crop year of 1990, this has been the main criteria for establishing matings after selections were done. Inbreeding has not accumulated more rapidly because an average of 16 bulls has been used for breeding in each of the last 4 mating periods.

**Table 4.** Levels of individual inbreeding accumulation that lead to inbreeding depression sufficient to cancel out one generation of genetic gain under weak selection pressure

<table>
<thead>
<tr>
<th>Trait</th>
<th>Heritability</th>
<th>Expected genetic gain per generation</th>
<th>Required inbreeding accumulation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birth weight, kg</td>
<td>0.395</td>
<td>0.41</td>
<td>0.187 ± 0.010</td>
</tr>
<tr>
<td>Weaning weight, kg</td>
<td>0.226</td>
<td>1.45</td>
<td>0.056 ± 0.004</td>
</tr>
<tr>
<td>Adjusted BW, 205 d, kg</td>
<td>0.281</td>
<td>1.72</td>
<td>0.068 ± 0.004</td>
</tr>
<tr>
<td>ADG, kg</td>
<td>0.260</td>
<td>0.0072</td>
<td>0.065 ± 0.004</td>
</tr>
<tr>
<td>Hock length, cm</td>
<td>0.412</td>
<td>0.112</td>
<td>0.018 ± 0.001</td>
</tr>
<tr>
<td>Scrotal circumference, cm</td>
<td>0.255</td>
<td>0.141</td>
<td>0.092 ± 0.010</td>
</tr>
</tbody>
</table>

1Weak selection pressure was defined as a selection intensity of 0.25.
2Values estimated by F. Siewerdt, J. A. Carrillo, and E. C. Draper (Wye Research and Education Center, Queenstown, MD; unpublished data).
3Accumulation in individual inbreeding. The reference point used was the predicted mean for a non-inbred animal using the exponential model; for hock length, the table values define the surface where established inbreeding depression is observed.
4This prediction uses a marginal solution that assumes no maternal inbreeding.
seasons, with an average of just under 10 calves per bull and few bulls with small progeny numbers.

Rumford-Newton is not an appropriate model to adequately describe the biology of the effect of inbreeding on preweaning traits. This was corroborated by the lack of success in obtaining convergence for the parameters of the model due to singular Hessians. When these second-order partial derivatives form a singular Hessian matrix, the Newton optimization algorithm becomes compromised and in cases of strict singularity no estimates for the parameters can be obtained (Magnus and Neudecker, 1999). The quadratic model, which is usually the first choice for a departure of linearity in inbreeding studies with livestock (Nelms and Stratton, 1967; Pariacote et al., 1998; McParland et al., 2007; Carolino and Gama, 2008; Casellas et al., 2009), did not show to be a reliable or meaningful option. In more than one-half of the models fitted the quadratic model was inadequate because of lack of statistical significance or because the fitted equation did not reflect a phenomenon that could be correctly explained by principles of population genetics. The greater robustness of prediction of the exponential model should make it preferable to the quadratic option.

Michaelis-Menten had greater fit to the data than the linear and exponential models for individual inbreeding, but fit was less for maternal inbreeding. The Michaelis-Menten model should be considered when greater levels of inbreeding exist. In the present study inbreeding depression for all traits at the extreme values of inbreeding was estimated to be, at most, 4.5% (individual) or 2.9% (maternal). When greater levels of inbreeding are present, the Michaelis-Menten model may provide an accurate representation of inbreeding depression if unfavorable epistatic effects are expressed. This model has a greater R² and can predict well at depression if unfavorable epistatic effects are expressed. The exponential model should be considered when great-

Even the best regression models in this study had small coefficients of determination, which carries, as a consequence, poor accuracy for predictions based on inbreeding values. This may have been observed due to elevated degree of variability in adjusted phenotypic observations within each inbreeding level. Alternatively, it may be the joint effects of selection and inbreeding that could not be properly separated in this particular herd by using the animal model.

The effect of individual inbreeding on WW was similar to the ones found by Nelms and Stratton (1967), Burrow (1998), and Carolino and Gama (2008) in the Alentejana breed; the coefficients reported by the first 2 sets of authors were not significantly different from zero, the former due to a very small sample size in Hereford cattle. The same pattern was found by those authors for maternal inbreeding, with the exception of Burrow (1998) who did not include maternal inbreeding in his study. Pariacote et al. (1998) observed individual and maternal inbreeding effects in Hereford cattle that were more than twice the size of those reported herein.

Birth weights in the present herd are considered adequate for the Angus breed; thus, selection would not aim at deliberately increasing WB. Inbreeding accumulation would result in a decrease of WB, but its impact will be low because WB was the trait that required the least selection effort to recover losses from inbreeding accumulation. The effects of individual and maternal inbreeding on WW were less than previous reports by Nelms and Stratton (1967) at 180 d old and Burrow (1998), comparable with those found by Carolino and Gama (2008) but much less that the effects given by Pariacote et al. (1998). Inbreeding depression affected SC at a reduced rate compared with the one reported by Burrow (1998). The structure of the Wye Angus herd has most animals with inbreeding values under 0.20; weak density of data at greater values of individual and maternal inbreeding does not allow for a sharp decrease in phenotypic values due to initial inbreeding accumulation. In populations that have initial high heterozygosity inbreeding depression will be observed even at low accumulation levels. The founder animals of the Wye herd, despite having originated from several genetic groups, share the same relatively narrow genetic base of a pure breed, whereas the population described by Burrow (1998) should show a much greater degree of initial variability for being a late generation of the cross between 4 European and zebu breeds.
For the current effective population size of the herd, the predicted rate of inbreeding accumulation is around 0.0085, which would imply that it would take about 7 generations for the inbreeding depression to accumulate to a critical value in growth traits. It was predicted that weak selection can be used to overcome the losses due to inbreeding depression in this herd. Validating this particular result with a selection experiment would support the idea that selection decisions should include a weak selection differential for those traits that are more influenced by inbreeding depression.

The SC is correlated with key reproductive traits in males and females (Toelle and Robison, 1985; Smith et al., 1989; Gregory et al., 1991; Kriese et al., 1991; Moser et al., 1996; Martínez-Velázquez et al., 2003). The decrease in SC can have an important economic impact on herd profitability, but at the current rate of inbreeding accumulation in the Wye herd it would take around 11 generations for inbreeding depression to become a relevant issue in SC.

Hock length is a measure of size of the animal frame. The interaction between the effects of individual and maternal inbreeding levels requires taking both measures into consideration when evaluating its effect on HL. A low combined amount of individual and maternal inbreeding accumulation is sufficient to reduce phenotypic values in HL, suggesting that even this trait which is traditionally thought as being not susceptible to inbreeding depression has to be considered in selection decisions. The observed interaction between individual and maternal inbreeding on HL may be an indicator that the 2 types of inbreeding may jointly influence other traits. Capturing this interaction would require elaborate experimental designs and the use of adequate higher-order multiple regression models to accurately search for alternative patterns of interaction. It is possible that more complex models could provide meaningful biological interpretation to the parameters of the ensuing equations.

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