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# The effect of inbreeding on racing performance in Norwegian cold-blooded trotters

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**Abstract** – The effect of inbreeding, i.e. the inbreeding coefficient, on racing performance, as measured by accumulated, transformed and standardised earnings (ATSE), was estimated either by linear or curvilinear regression, one variable at a time, in univariate animal models. The statistical model included, in addition, the effects of sex and birth year. Four ATSE variables, with information on earnings summed up over age-classes 3, 3–4, 3–5 and 3–6 years of age, were analysed. Only performances for horses born from 1972 onwards were used. For each animal, five inbreeding variables were calculated utilising ancestors for two (F2), three (F3), four (F4) and five (F5) generations or all available pedigree information (FTOT). Number of records used in analyses of ATSE3, ATSE3–4, ATSE3–5 and ATSE3–6 were 7 866, 7 866, 6 825 and 5 907, respectively. The estimated regressions, transformed to the standardised normal scale, were negative showing that racing performance was depressed by inbreeding. The best fit was for curvilinear regression. The pattern made up by the estimated regression coefficients indicated that selection was able to arrest some inbreeding depression over the first four generations, most likely due to recessive mutations, while additional purging of assumed mildly recessive mutations was shown to be a slower process. © Inra/Elsevier, Paris

horse / inbreeding depression / selection

**Résumé** – Effet de la consanguinité sur les performances en course chez les trotteurs Norvégiens. L'effet du coefficient de consanguinité sur les performances en course mesurées par les gains cumulés transformés et standardisés (ATSE) a été estimé par régression linéaire ou curvilinéaire, variable par variable, après utilisation de modèles animaux univariates, incluant les effets du sexe et de l'année de naissance. Quatre variables ATSE, avec l'information sur les gains cumulés à 3 ans, à 4 ans, à 5 ans, à 6 ans ont été analysées. Seules les performances des chevaux nés à partir de 1972 ont été utilisées. Pour chaque animal, cinq variables de consanguinité ont été

calculées en remontant sur 2 (F2), 3 (F3), 4 (F4), 5 (F5) générations ou sur l'ensemble du pedigree (FTOT). Les nombres de données utilisées dans les analyses de ATSE3, ATSE3-4, ATSE3-5 et ATSE3-6 ont été de 7 866, 7 866, 6 825 et 5 907 respectivement. Les régressions estimées, transformées sur une échelle normale standard, ont été négatives ce qui montre que les performances en course sont déprimées par la consanguinité. Le profil des coefficients de régression a indiqué que la sélection était capable d'amortir la dépression de consanguinité pendant les quatre premières générations quand elle était vraisemblablement due à des mutations récessives, tandis que l'élimination de mutations faiblement récessives s'est effectuée plus lentement.

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**cheval / dépression de consanguinité / sélection**

## 1. INTRODUCTION

The effect of inbreeding depression on racing performance of horses has mainly been examined in the former USSR on both Orlov trotters and Thoroughbreds. From Animal Breeding Abstracts, a tendency towards reduced performance upon inbreeding can be seen by comparing the phenotypic performance of inbred animals with that of outbreds [1, 13, 34-36, 40] or outbreds originating from the mating of inbred but unrelated parents [10-12]. The latter group should make up the most powerful contrast as it expresses some heterosis and inbreeding depression and heterosis, in a one-gene and biallelic situation, can be shown to be a complementary phenomenon with opposite signs [7]. The larger of these studies was that of Fomin et al. [13], including a total of 7 032 horses, while Fomin [11] based the results on 3 296 animals. The number of animals in inbred/outbred groupings was, respectively, 755/1 587, 1 290/721 and 1 176/148 in the studies of Rozhdestvenskaya [40], Pern [36] and Fomin [12]. Afanasjev [1] used 606 horses in the comparison, while the exact numbers included in the studies of Fomin [10], Pern [35] and Odnoletkova [34] were not given. Of the USSR studies, only one did not report any effect of inbreeding depression on racing performance [39]. It was, in fact, accepted in the USSR that inbreeding depressed performance [37]. One, therefore, operated with different limits for inbreeding depression to appear in different breeds [37]. Relevant studies have also been carried out in other countries, but on a too limited number of animals for clear conclusions to be drawn [28, 38]. A historical treatment of the subject was given by Flade [9].

From this short review, one may suspect that inbreeding negatively affects racing performance. Many of the references are not readily available, and a revisitation of the subject can now, therefore, be justified. The main goal of this study was, therefore, to estimate the effect of inbreeding on racing performance.

The Norwegian cold-blooded trotters should be well suited for such a purpose as the pedigree for horses born from 1972 until 1986 was complete for five ancestral generations in 62.8 % of all animals [24]. Racing performance data are also available over the same period and have been used to estimate additive (co)variance components of accumulated, transformed and standardised earnings (ATSE) among parents born prior to 1972 [25]. When this information was applied to an animal model [25], a considerable additive genetic trend was observed. This implies, according to Uimari and Kennedy [42], that the

effect of inbreeding on racing performance should be estimated simultaneously to effect(s) taking account of the selection response.

Uimari and Kennedy [42] and de Boer and van Arendonk [5] examined the estimation of inbreeding depression under phenotypic selection by stochastic simulation. Complete dominance was assumed for a finite locus model in both studies. Data were analysed by including both the dominance effect, ignoring inbreeding, and an additive genetic effect in addition to a linear regression of performance on the coefficient of inbreeding. Alternatively, Uimari and Kennedy [42] omitted the dominance effect from the model. At a given frequency of the favourable allele of 0.5 in the base population, inbreeding depression estimates were seemingly unbiased, while a frequency different from 0.5 resulted in somewhat biased estimates of inbreeding depression. Elimination of the dominance effect from the model reduced bias somewhat and increased depression, although still an underestimate. The bias was due to gene frequency changes under the finite locus model and, thus, not relevant for the infinitesimal model, where gene frequencies are assumed stable under selection [17].

Models including the additive genetic effect, a linear regression of performance on inbreeding and either including or excluding the dominance effect have been compared on field data [31, 32]. In both studies, only a tendency towards increased inbreeding depression was obtained from the simpler of the two models. Therefore, Miglior et al. [31] recommended the use of as simple a model as possible when the objective is solely to estimate inbreeding depression. This indicates that a model including the regression of performance on inbreeding and the animal effect should be adequate. Furthermore, the similarity in the inbreeding depression estimates obtained by Miglior et al. [31] made the authors suggest that the gene frequency in actual populations may be, on average, close to 0.5.

Fikse et al. [8] have reported the estimates of inbreeding depression from an animal model to be seriously affected by the data structure. The structure examined was one with the data known for the last generation only, and with the pedigree known for several generations. This structure is also relevant to the Norwegian cold-blooded trotters as racing performance data have been sampled over a much shorter time than pedigree records. Fikse et al. [8] claimed their problem to be due to the assignment of an erroneous genetic variance in later generations. When analysing ATSE, a trait that is standardised annually with an animal model, estimation of an unbiased genetic trend depends on inclusion of a birth year effect in the model [25]. If a complete animal model taking account of all additive relationship between animals relative to a distant base population is used, the model will estimate additive genetic values among animals without records. The additive genetic values of animals with records will be scaled by these values. This results in an overestimation of inbreeding depression. To avoid this problem, a logical base in the animal model is a closer base.

Another problem with relevance to estimation of inbreeding depression is the effect of selection [7, 8]. This is relevant to the Norwegian cold-blooded trotters as phenotypic selection has been widely practised. Under a finite locus model, selection will affect gene frequencies, and the bias will depend on the true underlying and unknown genetic model [17]. If inbreeding depression is partially due to a limited number of recessive mutations, as assumed by

Lande [29], selection may purge the population of some of its mutational load [7]. Therefore, the largest relationship between inbreeding and performance is expected when regressing performance on inbreeding coefficients calculated from a small number of ancestral generations. The second objective of this study was to estimate these regressions and to compare them with the available data.

## 2. MATERIALS AND METHODS

Klemetsdal [24] generated, by use of the horse register as filed by the Norwegian Trotting Association in 1986, several files in which horses born from 1972 until 1986 had all ancestors known for a fixed number of generations. For each animal, the files kept the identification of the individual generating the pedigree and, in addition, individual identification, renumbered individual, sire and dam identifications, generation number and year of birth. A total of 7 897 out of 12 569 horses born from 1972 onwards had all ancestors known for five generations, building up a dataset of altogether 244 807 records. This dataset was assumed to best fit the requirement for the largest possible pedigree depth with the highest possible number of animals. As ancestors had been accumulated within animal, calculation of each animal's inbreeding coefficient could easily be made for a variable pedigree depth, one horse at a time, by use of the Quaas-Henderson algorithm [21, 41]. The resulting variables, utilising ancestors in two (F2), three (F3), four (F4) and five (F5) generations, were merged onto the original dataset and kept for records with individual identification equal to the identification of the animal generating the pedigree.

Klemetsdal [24] also computed individual inbreeding coefficients for the 12 569 horses born from 1972 onwards. As all available pedigree information was used in that calculation, the corresponding inbreeding variable (FTOT) for the emphasised 7 897 horses is a measure of individual inbreeding given that all ancestors are known for at least five generations. FTOT was merged with the data in the same way as for the variables F2–F5. Finally, original sire and dam identifications were added to the generated dataset.

The considered racing performance variable was ATSE. ATSE is the power transformation of earnings (earnings 0.2, with unraced horses assigned a value of zero) expressed as a standardised normal deviate by birth year [22, 23]. The utilised records were those generated by Klemetsdal [24]. These were constructed by combining annually summarised totalizator race records documented within Norway with information on non-exported and Norwegian bred horses from the horse register in 1991. A total of four racing performance variables were available (ATSE3, ATSE3–4, ATSE3–5 and ATSE3–6 summarised over age-classes 3, 3–4, 3–5 and 3–6 years of age, respectively), and individual information for each variable was, successively, merged with the variable identifying the animal generating the pedigree. Information on the animals' sex was also added in one merging.

Racing performance data were available for horses born between 1972 and 1986 as data from 1975 to 1990 had been summarised on a yearly basis, and horses were first raced at 3 years of age [24]. Therefore, all horses born in 1986 or earlier were at least 4 years old in 1990 and had, thus, data for both ATSE3 and ATSE3–4. Similarly, ATSE3–5 was available for horses born in 1985 and earlier, while ATSE3–6 was restricted to horses born prior to 1985. The

number of racing performance data for horses having individual identification equal to the identification of the animal generating the pedigree is summarised in *table I*. The table shows that 31 out of 7 897 horses were observed with missing phenotypic data. In fact, 29 out of the 31 horses were omitted due to exportation, and the two remaining horses did not exist in the 1991 version of the horse register. *Table II* shows the number of horses per birth year class. The table demonstrates, as expected, an increased number of observations with time, and, furthermore, that, for example, the number of observations in 1986 corresponded exactly with the reduction in number of observations for ATSE3-5 relative to those for ATSE3-4, as given in *table I*.

**Table I.** Number of data and pedigree records used in analyses of four accumulated, transformed and standardised earning (ATSE) variables for horses born between 1972 and 1986 with an animal model.

| ATSE variable <sup>a</sup> | Summation of earnings over age-class(es) <sup>b</sup> | Data records | Pedigree records   |                |
|----------------------------|---|--------------|--------------------|----------------|
|                            |   | <i>n</i>     | non-base, <i>n</i> | base, <i>n</i> |
| ATSE3                      | 3   | 7 866        | 8 797              | 1 788          |
| ATSE3-4                    | 3-4   | 7 866        | 8 797              | 1 788          |
| ATSE3-5                    | 3-5   | 6 825        | 7 620              | 1 743          |
| ATSE3-6                    | 3-6   | 5 907        | 6 577              | 1 693          |

<sup>a</sup> Earnings were power transformed (0.2) and expressed as a standardised normal deviate by birth year. <sup>b</sup> Unraced horses were assigned a value of 0, i.e. zero earnings.

Inbreeding depression was estimated by an animal model and taken out as the regression of racing performance on inbreeding. By use of regression, a distant base relative to animals with data, as studied by Fikse et al. [8], may inflate the size of the regression if there exists genetic trend for the trait under study. As this was assumed to be the situation for racing performance, but also because the available variance component estimates referred to a base comprising parents with progeny born from 1972 onwards, themselves born prior to 1972 [25], the same definition of the base was chosen for the animal model in this study. To obtain pedigree records with this base, all individuals born from 1972 onwards being marked with the existence of a phenotypic record for the animal generating the pedigree were kept, while duplicate records were all deleted. *Table I* shows the number of base and non-base animals, with the latter being larger than the number of horses having performance records as all ancestors born between 1972 and 1986 were included in the pedigree data. The number of such ancestral records amounted to 931 for both ATSE3 and ATSE3-4, 795 for ATSE3-5 and 670 for ATSE3-6.

The univariate animal model included in addition to the random additive animal effect  $\sim(0, A\sigma_a^2$ ; where  $A$  is the additive genetic relationship matrix corrected for possible inbreeding from the assumed base onwards, and  $\sigma_a^2$  is the additive genetic variance), a random residual term  $\sim(0, I\sigma_e^2$ ; where  $I$  is an identity matrix and  $\sigma_e^2$  is the residual variance), fixed effects of birth year and sex and either a linear (L) or curvilinear (C) effect for the calculated inbreeding variables, one at a time.

**Table II.** Frequency distribution of ATSE records by birth year and sex classes.

| Factor with classes |        | ATSE3 and ATSE3-4  |
|---------------------|--------|--------------------|
| Birth year:         | 1972   | 154                |
|                     | 1973   | 189                |
|                     | 1974   | 257                |
|                     | 1975   | 330                |
|                     | 1976   | 391                |
|                     | 1977   | 427                |
|                     | 1978   | 494                |
|                     | 1979   | 539                |
|                     | 1980   | 528                |
|                     | 1981   | 576                |
|                     | 1982   | 572                |
|                     | 1983   | 685                |
|                     | 1984   | 765                |
|                     | 1985   | 918                |
|                     | 1986   | 1 041 <sup>a</sup> |
| Sex:                | female | 4 011 <sup>b</sup> |
|                     | male   | 3 855              |

<sup>a</sup> ATSE3-5 records were not available for horses born in 1986, while ATSE3-6 records were missing for horses with birth year 1985 and 1986. <sup>b</sup> Frequency distribution: ATSE3-5: female 3 509; male 3 316; ATSE3-6: female 3 056; male 2 851.

The animal model was fitted by use of the PEST program [18]. The regression coefficients were tested against zero by use of the program's hypothesis testing procedure [19, 20] resulting in an ordinary F-test relevant for a linear model. The corresponding numerator and denominator degrees of freedom were 1 and the total number of observations minus the rank of the fixed effects, respectively.

As the same phenotypic records were regressed on the different inbreeding variables with a steady increase of variance with pedigree depth, the resulting regression coefficient estimates were not directly comparable. Direct comparison and inference should only be made on the basis of estimates resulting from inbreeding variables scaled to have the same variance. The standardised normal scale was chosen as there is a simple relationship between estimates on the two scales. According to Weisberg [43], the scaling does not affect the F-test values, and the scaled regression coefficient estimates were obtained by multiplying the regression coefficient estimate on the original scale by the standard deviation of the corresponding inbreeding variable. By analogy, the variance of the scaled estimate was computed as the variance of the original estimate multiplied by the variance of the inbreeding variable.

The contrasts between estimated regression coefficients on the standardised scale ( $\beta$  and  $\beta^*$ ), related to linear modelling of depression, were tested by use of the following one-tailed *t*-test:

$$t = (\beta - \beta^*) / \text{se}(\beta - \beta^*)$$

where:

$$\text{se}(\beta - \beta^*) = \sqrt{\text{Var}(\beta - \beta^*)}$$

with:

$$\text{var}(\beta - \beta^*) = \text{var}(\beta) + \text{var}(\beta^*) - 2\text{cov}(\beta, \beta^*)$$

The two variances were animal model estimates, while the covariance was approximated as the expectation of the product of their least square estimates as relevant for simple linear regression. The covariance was shown equal to:

$$\text{cov}(\beta, \beta^*) = \sigma_e^2 \left( \sum (F_i - \bar{F})(F_i^* - \bar{F}^*) / \sum (F_i - \bar{F})^2 \sum (F_i^* - \bar{F}^*)^2 \right)$$

where  $F$  and  $F^*$  are two different and scaled inbreeding coefficients of the same animal, and  $\sigma_e^2$  is an estimate of the two models' average residual variance.

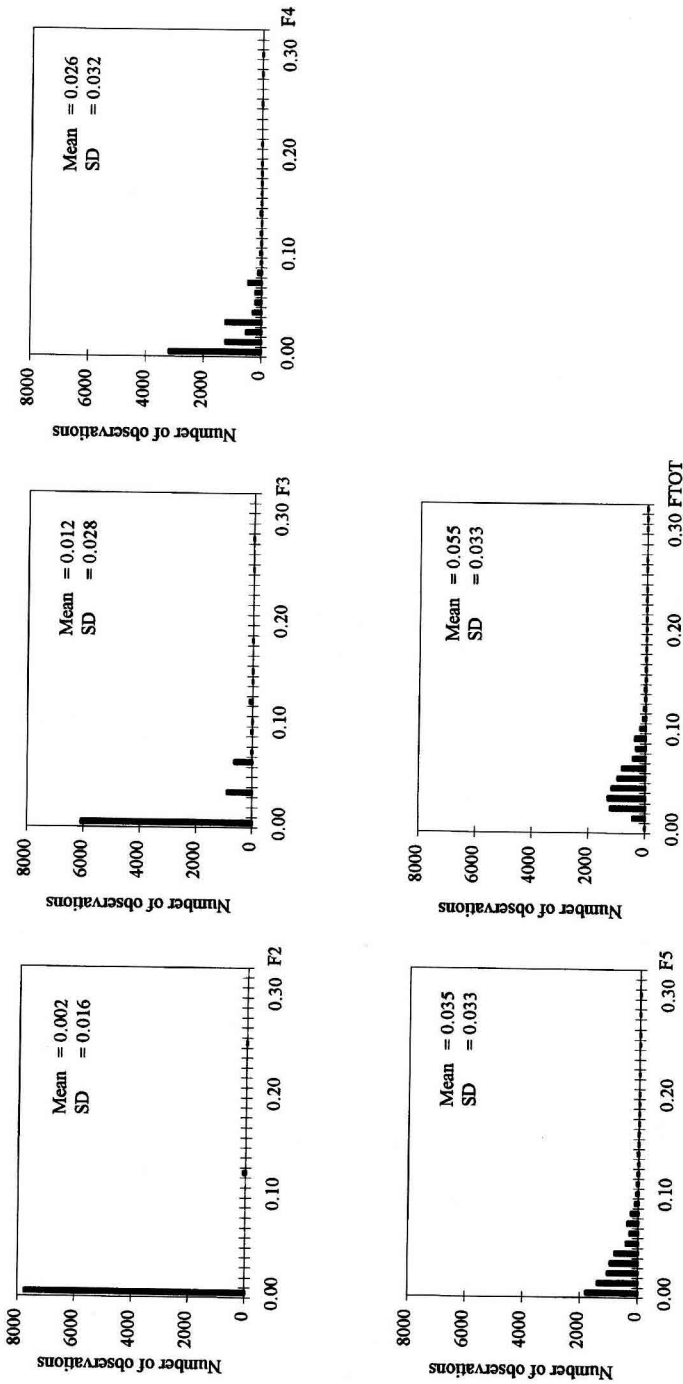
Finally, inbreeding depression sensitivity was examined by increasing or decreasing the additive genetic variance by 0.10 units at an unchanged phenotypic variance.

### 3. RESULTS

The distributions of the different inbreeding variables are shown in *figure 1*. The frequency of inbred animals increased with inclusion of a steadily larger number of ancestral generations. All animals were, in fact, inbred when all ancestral information was included in the calculation of the inbreeding coefficients. Corresponding fractions for F2, F3, F4 and F5 were 0.01, 0.23, 0.72 and 0.94, respectively.

The estimated regressions, either linear or curvilinear, of racing performance on inbreeding were generally negative (*table III*) implying inbreeding depression. The relationship was for the most part significant ( $P < 0.05$ ). The exceptions were the regression of ATSE variables on F2, as only 110 animals were inbred, and the linear regression of ATSE3 on F5 and FTOT. The quadratic regression of the latter relationships were, however, significant indicating an improved fit of quadratic modelling over linear modelling of inbreeding. Formally, the regression sums of squares equals the product of the F-test value and the residual error variance. As the latter was approximately equal in both linear and curvilinear modelling of inbreeding depression for the same trait and inbreeding variable, an enlarged F-test value also indicates an improved fit. The F-test values were in favour of curvilinear modelling for inbreeding variables F4, F5 and FTOT (*table III*), while linear modelling was shown to be preferable for F3. The curvilinear relationship between racing performance and inbreeding is illustrated in *figure 2*.

Although the regression coefficient estimates in *table III* are relevant when calculating actual inbreeding depression given different amount of pedigree information, direct comparison of regression coefficient estimates was carried out on the basis of standardised inbreeding variables. The estimates are given in *table IV*. Both under linear and curvilinear modelling of depression, the least negative inbreeding depression estimates were obtained for the standardised inbreeding variable resulting from F2, while the largest estimates, in general, were those for the standardised F4 variable. Under linear modelling of depression, inclusion of another pedigree generation resulted in a marked drop



**Figure 1.** Frequency distribution of inbreeding coefficients for horses with all ancestors known for at least five generations making up the 7 866 individuals with records for ATSE3 and ATSE3-4 in *table 1*. The figures refer to inbreeding variables calculated by use of ancestral information in two (F2), three (F3), four (F4) and five (F5) generations, while all available pedigree information was included in calculation of FTOT.

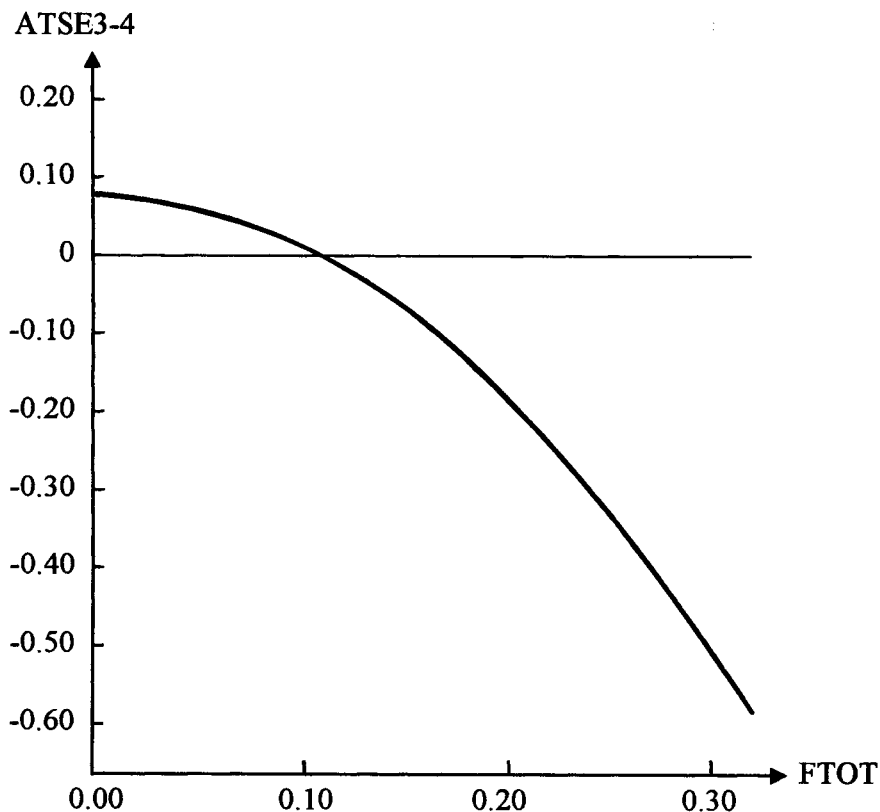
**Table III.** Regression coefficient estimates ( $\beta$ ) of ATSE on 100 % inbreeding under linear and curvilinear modelling of inbreeding depression, their standard error (s.e. ( $\beta$ )), test statistics ( $F$ ) and level of significance ( $p$ ).

| ATSE variable | Inbreeding variable | Linear  |                  |       |       | Curvilinear |                  |       |       |
|---------------|---------------------|---------|------------------|-------|-------|-------------|------------------|-------|-------|
|               |                     | $\beta$ | s.e. ( $\beta$ ) | $F$   | $p$   | $\beta$     | s.e. ( $\beta$ ) | $F$   | $p$   |
| ATSE3         | F2                  | -0.91   | 0.70             | 1.67  | 0.196 | -5.70       | 4.18             | 1.86  | 0.172 |
|               | F3                  | -1.02   | 0.43             | 5.73  | 0.017 | -7.25       | 3.24             | 5.03  | 0.025 |
|               | F4                  | -0.89   | 0.39             | 5.14  | 0.023 | -7.35       | 2.70             | 7.43  | 0.006 |
|               | F5                  | -0.68   | 0.38             | 3.19  | 0.074 | -6.24       | 2.43             | 6.59  | 0.010 |
|               | FTOT                | -0.62   | 0.39             | 2.59  | 0.107 | -4.99       | 2.04             | 6.00  | 0.014 |
| ATSE3-4       | F2                  | -1.16   | 0.69             | 2.87  | 0.090 | -7.24       | 4.10             | 3.12  | 0.078 |
|               | F3                  | -1.26   | 0.42             | 8.91  | 0.003 | -8.92       | 3.18             | 7.87  | 0.005 |
|               | F4                  | -1.16   | 0.39             | 8.95  | 0.003 | -9.06       | 2.66             | 11.60 | 0.001 |
|               | F5                  | -0.85   | 0.38             | 5.03  | 0.025 | -7.81       | 2.40             | 10.60 | 0.001 |
|               | FTOT                | -0.85   | 0.38             | 4.91  | 0.027 | -6.44       | 2.01             | 10.30 | 0.001 |
| ATSE3-5       | F2                  | -1.28   | 0.69             | 3.40  | 0.065 | -8.13       | 4.11             | 3.92  | 0.048 |
|               | F3                  | -1.77   | 0.44             | 16.50 | 0.000 | -11.34      | 3.21             | 12.50 | 0.000 |
|               | F4                  | -1.67   | 0.40             | 17.20 | 0.000 | -11.21      | 2.70             | 17.30 | 0.000 |
|               | F5                  | -1.33   | 0.39             | 11.40 | 0.001 | -9.84       | 2.44             | 16.20 | 0.000 |
|               | FTOT                | -1.35   | 0.40             | 11.60 | 0.001 | -8.46       | 2.06             | 17.00 | 0.000 |
| ATSE3-6       | F2                  | -1.21   | 0.72             | 2.76  | 0.097 | -8.13       | 4.21             | 3.72  | 0.054 |
|               | F3                  | -1.94   | 0.46             | 17.70 | 0.000 | -12.10      | 3.31             | 13.40 | 0.000 |
|               | F4                  | -1.75   | 0.42             | 17.00 | 0.000 | -12.12      | 2.79             | 18.80 | 0.000 |
|               | F5                  | -1.38   | 0.41             | 11.10 | 0.001 | -10.63      | 2.54             | 17.60 | 0.000 |
|               | FTOT                | -1.38   | 0.42             | 11.00 | 0.001 | -8.95       | 2.14             | 17.50 | 0.000 |

<sup>a</sup> ATSE3-5 records were not available for horses born in 1986, while ATSE3-6 records were missing for horses with birth year 1985 and 1986. <sup>b</sup> Frequency distribution: ATSE3-5: female 3 509; male 3316; ATSE3-6: female 3 056; male 2 851.

of the estimated inbreeding depression, while additional pedigree information only reduced depression to a minor degree. This reduction in size of regression coefficients for the standardised F4 variable versus the corresponding FTOT variable was tested by a  $t$ -test. The largest  $t$ -value was obtained for ATSE3-6, however, not significant ( $P < 0.18$ ). Similar testing was not carried out under curvilinear modelling of inbreeding depression as depression actually increased for one of the racing performance variables, ATSE3-5. A tendency towards reduction was, however, observed for the other ATSE variables.

The contrast giving rise to the largest  $t$ -value under linear modelling of inbreeding depression was examined for its sensitivity to changed genetic parameters. At an unchanged phenotypic variance, an increase or decrease in additive genetic variance of 0.10 units relative to the assumed value increased or decreased the inbreeding depression (*figure 3*). The changes, however, were small, and the estimated regression coefficients were all highly negative and significantly different from zero ( $P < 0.005$ ). The size of the contrasts was also robust to changed additive genetic variance, while the  $t$ -values and, hence, the



**Figure 2.** The curvilinear relationship between ATSE3-4 and FTOT as averaged over sex, birth year and animal effects.

levels of significance were somewhat affected by this assumption. A reduction of the assumed additive genetic variance increased the probability of a real difference between the estimated regression coefficients ( $P < 0.11$ ).

#### 4. DISCUSSION

The results demonstrate that racing performance in Norwegian cold-blooded trotters is depressed by inbreeding. In size, the estimates from linear modelling of inbreeding depression were a factor 0.55 of the largest estimates reported by Klemetsdal and Stubbsj en [27]. Relative to the current study, Klemetsdal and Stubbsj en [27] utilised all available pedigree information and a more remote base in the BLUP analyses which inflated the inbreeding depression estimates. They did not find any significant effect of the dams' inbreeding coefficient, and this effect was, therefore, left out from the statistical model used in this study.

The least negative estimates of inbreeding depression were obtained when two ancestral generations were used to calculate the inbreeding coefficients. This can be explained by underestimation due to inclusion of horses, actually

**Table IV.** Regression coefficient estimates ( $\beta$ ) on the standardised normal scale of ATSE on 100 % inbreeding under linear and curvilinear modelling of inbreeding depression.

| ATSE variable | Standardised inbreeding variable resulting from | Linear $\beta^a$ | Curvilinear $\beta^b$ |
|---------------|---|------------------|-----------------------|
| ATSE3         | F2  | -0.015           | -0.016                |
|               | F3  | -0.028           | -0.026                |
|               | F4  | -0.028           | -0.033                |
|               | F5  | -0.022           | -0.031                |
|               | FTOT  | -0.020           | -0.030                |
| ATSE3-4       | F2  | -0.019           | -0.020                |
|               | F3  | -0.035           | -0.032                |
|               | F4  | -0.037           | -0.040                |
|               | F5  | -0.028           | -0.039                |
|               | FTOT  | -0.028           | -0.038                |
| ATSE3-5       | F2  | -0.022           | -0.024                |
|               | F3  | -0.051           | -0.043                |
|               | F4  | -0.054           | -0.052                |
|               | F5  | -0.045           | -0.051                |
|               | FTOT  | -0.045           | -0.052                |
| ATSE3-6       | F2  | -0.022           | -0.025                |
|               | F3  | -0.056           | -0.048                |
|               | F4  | -0.057           | -0.058                |
|               | F5  | -0.047           | -0.057                |
|               | FTOT  | -0.046           | -0.057                |

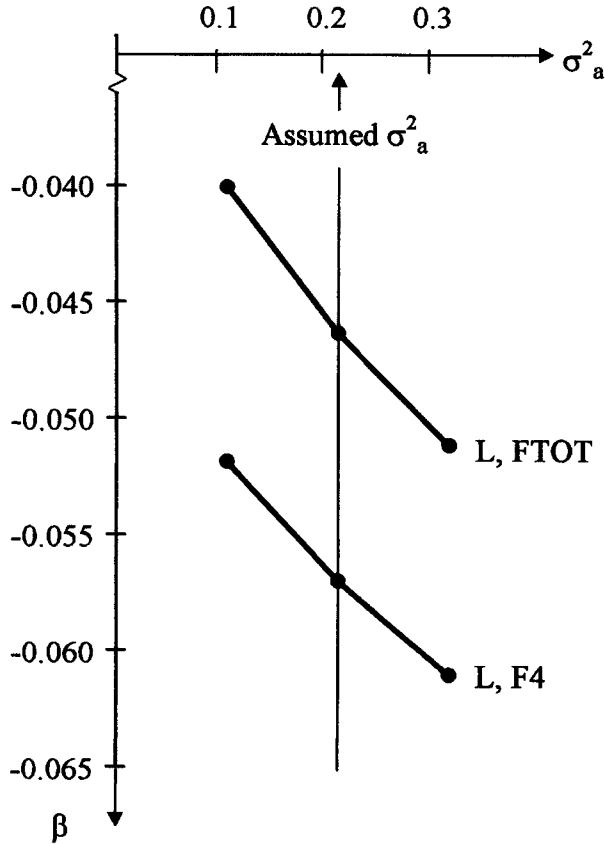
<sup>a,b</sup> The standard error (s.e. ( $\beta$ )) ranged between 0.011 and 0.014.

inbred, as outbred in analyses which given a negative effect upon inbreeding will reduce the estimated regressions.

This effect may also explain the reduced depression for the standardised F3 variable relative to the corresponding F4 variable, which for the same reason may be beyond their true values.

Relative to the F4 estimates obtained under linear modelling of inbreeding depression, the corresponding estimates for F5 were considerably reduced. Further reduction in size of estimates was hardly observed when regressing on the standardised FTOT variable. This pattern is consistent with selection eliminating lethals and sublethal mutations in course of the first four generations. Additional purging of mildly recessive mutations is a slower process and in agreement with the current knowledge in this field, reviewed by Lande [29].

Although there exists strong indications that selection is able to arrest some inbreeding depression over time, the formal testing of selection, carried out by contrasting regression coefficient estimates under linear modelling of depression, did not reveal any significant effect. The test, however, is lacking power as the F4 estimates may be below their true values, also because of selection, and the standardised FTOT variable gives upper limit estimates, as partially the same



**Figure 3.** Regression coefficient estimates of ATSE3-6 on inbreeding variables F4 ( $\beta_{L,F4}$ ) and FTOT ( $\beta_{L,FTOT}$ ) under linear modelling of inbreeding ( $L$ ) for an increased or decreased additive genetic variance ( $\sigma_a^2$ ) of 0.10 units relative to the assumed value, at an unchanged phenotypic variance.

ancestral information was used to calculate both F4 and FTOT, resulting in a contrast that is a lower limit estimate of the ability of selection to purge inbreeding depression. An effect of selection may, therefore, be truly present without being detected by this test. Hence, there is a need for developing alternative methodology to test the effect of selection on inbreeding depression. One alternative approach is that proposed by Ballou [2].

Modelling of a curvilinear effect of inbreeding depression showed, in general, an improved fit over similar linear modelling. This indicates that the effect of inbreeding depression on racing performance depends on the level of inbreeding. A certain increase in the coefficient of inbreeding at a low level of inbreeding will, therefore, affect racing performance less from inbreeding depression than at a higher level of inbreeding. The low inbreeding coefficients are mainly due to distant inbreeding, and the small inbreeding depression at this level supports the earlier finding of an effect of selection on inbreeding depression, although

the estimated regression coefficients were not, generally, reduced for F5 and FTOT relative to F4.

Lande [29] assumed that inbreeding depression, not explained by lethal and sublethal mutations, was mainly due to mildly recessive mutations. These may be assumed to express partial dominance. By taking on other reasonable assumptions as a finite locus model, an average gene frequency in the base population close to 0.5 and phenotypic selection, the gene frequency based inbreeding coefficients are larger than the pedigree based counterpart [17]. The difference between the two coefficients was shown to increase over generations, that it, on average, became larger for a higher inbreeding coefficient. The most expressed inbreeding coefficients, in this study, were those of FTOT implying that inbreeding depression may have been somewhat overestimated and to the largest extent for FTOT. Consequently, the contrasts between inbreeding depression estimates may also, due to this logic, be larger in reality than estimated.

Another factor which could influence the inbreeding depression estimates is the effect of birth year. The use of equal number of ancestral generations in calculation of inbreeding coefficients for all horses irrespective of birth year ensures a reasonable orthogonality between the two effects. They are, therefore, most likely efficiently separated in analyses.

The result reported here is another indication that selection is able to counteract a significant part of inbreeding depression over time, as shown and discussed for fitness related traits by Frankham et al. [14]. Related is the recent interest shown in counteracting fitness reduction in a breeding program from culling breeding animals on a basis of parental information on fitness related traits, in a first stage, and then concentrating on improving production traits in the second stage [15, 16, 30].

To illustrate the effect of inbreeding depression on racing performance, the curvilinear estimates obtained for FTOT are most relevant as they include both close and remote inbreeding. A doubling of the inbreeding coefficient will then, at all inbreeding levels, quadruplicate depression. As the average inbreeding coefficient in the population today may be assumed close to 7.5 %, the average ATSE3-4 performance, for example, is expected to be depressed by 0.036 phenotypic standard deviation. Horses inbred to 15 %, however, are four times as much depressed amounting to 0.145 phenotypic standard deviation units. Correspondingly, the most inbred animal in the material, having an FTOT value of 32 %, is expected to perform 0.66 standard deviation units beyond a non-inbred animal. This is a significant handicap which should motivate avoidance of close matings, or, alternatively, the use of minimum coancestry mating which, additionally, is expected to reduce the rate of inbreeding in the population [3, 26]. Minimum coancestry mating involves mating of individuals that are less related than the average in the population. Therefore, it is a mild form of crossbreeding for which some heterosis is expected [7], and which should further motivate its use.

Inbreeding depression was assumed absent in the search for static selection rules relevant for selecting sires on a basis of ATSE breeding values in the North-Swedish and Norwegian cold-blooded trotter populations [26]. Inbreeding depression, however, could have been taken into account by expressing the

results in phenotypic standard deviation units [6]. This would have affected the results in direction of a smaller favourable progeny group size of sires.

Inbreeding depression is one of five genetic parameters describing the complete genetic covariance due to dominance under inbreeding (e.g. [4]). To estimate two of these parameters, i.e. in addition to inbreeding depression also the dominance variance (ignoring the effect of inbreeding on dominance relationships), with a reasonable sampling variance would require a substantial amount of data (hundreds of thousands) [32]. The large number is due to the limited number of dominance relationship for species with a low reproductive rate such as the horse. Hence, the genetic improvement of small horse populations, such as the North-Swedish and Norwegian cold-blooded trotter populations, has to rely on the additive genetic variance also in the foreseen future.

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