Ann Zootech (1996) 45, 41-51

Original article

A consideration of the genetic aspects of some current practices in Thoroughbred horse breeding

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(Received 16 November 1994; accepted 17 May 1995)

Summary — The genetic problems involved in Thoroughbred breeding are reviewed. First, an historical and sociological analysis highlights the following questions: Is performance selection, the great historical contribution of Thoroughbred breeding, still effective? Is breed purity a myth or a technically effective reality? What about inbreeding? What are the respective influences of the mare and stallion? Second, the answers put forth by the scientific community are examined. Finally, consideration is given to future prospects and to the progress required for genetic management in an industry where the concepts currently in use are very outdated.

horse / Thoroughbred / racing ability / selection

Résumé — Considérations sur les aspects génétiques de quelques pratiques courantes dans l'élevage du cheval de pur sang. *Les problèmes génétiques soulevés par l'élevage du pur-sang sont examinés. Dans un premier temps, l'analyse historique et sociologique décrit les questions posées. Dans une seconde partie, les réponses de la communauté scientifique à ces interrogations sont passées en revue. La sélection sur les performances, grande innovation historique de l'élevage du pur-sang, est-elle toujours efficace ? La race pure est-elle un concept mythique ou une réalité efficace ? Que penser de* l'inbreeding*? Quels sont les rôles respectifs de l'étalon et de la poulinière ? On conclut sur les perspectives ouvertes et en particulier sur les progrès à faire en matière de gestion génétique où les conceptions en vigueur sont très passéistes.*

cheval / pur-sang / aptitude à la course / sélection

INTRODUCTION

Horse breeding has its historical and sociological dimension, in which the emergence of the English Thoroughbred was a major innovation, an event of prime importance for the development of the art and which was and continues to be a frequent focus of controversy. It therefore seems important (Langlois, 1991) to situate the achievements of Thoroughbred breeding historically, so as to highlight the main questions raised. We shall then examine the answers scientists currently propose, and conclude with a consideration of future prospects.

THE QUESTIONS RAISED

The concepts of blood, breed purity, selection and improvement have important historical and sociological implications which, today, make any approach to the question of genetic improvement in the Thoroughbred a delicate matter. The notion of 'improvement of the equine species' is therefore of very great cultural importance. According to Mulliez (1983), the expression dates back to the articles on the horse and donkey in Buffon's *Histoire Naturelle* of 1753. Despite the very strong imprint of the creationist dogmas of the time, these articles prefigured evolutionist ideas in their use of the concept of degeneration of a breed due to the influence of place or climate. These ideas were adopted by the highly authoritative Bourgelat, founder of the French veterinary colleges, in the cross-breeding doctrine he imposed on the fledgeling administration of the national stud farms. To return to the ideal type of the Creation, as defined by his famous canons, he recommended choosing a stallion of the opposite type to the dam, to compensate for the divergence of her traits from the perfect ideal. This meant seeking out stallions in distant lands or regions.

It was only later, when Darwinian thinking on evolution introduced the concept of selection, that the idea of improving the native population emerged to counterbalance this and effectively replace the desire for merely conserving local types. The creation of the English Thoroughbred further reinforced these ideas, also imposing the idea of selecting for performance rather than for appearance.

Thereafter, purebred management gradually came to predominate over cross-breeding, culminating in the establishment of the Stud or Herd Books, a key feature of animal production techniques in the ninetheenth century. These techniques required precise identification procedures so that racing records achieved at different times and in different places could be related to the same horse. The Stud Books, by certifying lineage, made it possible to link performance not only to the horse itself but also to its relatives. This opened the way to genealogical selection and progeny testing. The respective roles of the mare and the stallion could be examined from the records, giving rise to a new notion, that of the 'dam-sire'. The emphasis on the female line (dam to granddam, etc), whether justified or unjustified, also made it possible to reactivate the concept of crossing different lines in the management of purebred stock. Efforts for 'inbreeding' and 'outbreeding' triggered the same mechanisms. Since both were based on the belief that there is something to gain from the assortment of the mates that could not be obtained by random mating of selected mares and stallions.

Until the dawn of the twentieth century, the horse – with which men identified very closely – was the sole focus for experimental testing of heredity theories. However, these theories developed in line with the sociological support they received.

While not wishing to advance any further into the human sciences, we shall recapitulate the principal notions introduced, historically, by Thoroughbred breeding:

– selection on performance within a pure breed;

– the introduction of precise management of identity and lineage through the Stud Book;

– reflection on the respective roles of mare and stallion;

– generalized use of planned mating.

Are the ideas and customs of Thoroughbred breeding circles in these areas still justified? What have the scientific community to say about these questions today?

VIEWPOINT OF THE SCIENTIFIC COMMUNITY

Is performance selection, historically the great innovation of Thoroughbred breeding, still effective?

In 1988 this question hit the headlines in Europe and America after a controversy between Gaffney and Cunningham, and Hill in the April issue of *Nature*. The problem is as follows: despite the intensity of selection carried out in the Thoroughbred, race times have not improved any further for at least the past 50 years (Hamori and Halasz, 1959; Cunningham, 1975). And yet the most commonly used selection criteria, handicap weights and prize money, generally have a high heritability rating ($0.3 < h^2 < 0.4$) according to bibliographical reviews (Langlois, 1975, 1980; Hintz, 1980; Tolley et al, 1985). There is thus an apparent contradiction between this selection for a heritable trait and the failure to translate this into faster track performance. There are two ways to study this paradox:

The first is fairly theoretical, involving a search for the reasons why heritability could be overestimated, the main reason being that apparent variability has become greater than real variability because certain genetic effects are systematically associated owing to the generalized practice of assortative mating. This phenomenon, known as *homogamy*, engenders linkage disequilibrium, ie, a kind of genetic variability due to associations of genes in addition to the common variability resulting from the effects of the genes. The traditional methods of estimating heritability should, in fact, be corrected for this phenomenon (Langlois, 1981). Thus, genetic variability does not simply result from the variability of the genes at each locus, but also from covariance among the effects of these genes.

It is likely that correlation between genetic and environmental effects is a further source of overestimation. How can one be certain that environmental effects on offspring are independent of the parental genotypes? Surely it is the offspring of top-grade breeding stock that will be predestined for a top-grade training establishment, improving their chances of a brilliant racing career? In our opinion, the great importance of the trainer effect revealed by Schulze-Schleppinghoff et al (1985, 1987) and Preisinger et al (1989, 1990) is a reflection of this phenomenon. And yet the general opinion seems to be that all young Thoroughbreds are subjected to the same training tasks each day, so that they are all in a standard condition of physical preparation which some experts (d'Orsetti, 1993) consider too basic, although they acknowledge that it is hard to do better with young, growing horses.

With regard to these two phenomena – nonrandom mating and the nonindependence of genetic and environmental effects (also encountered in studies of the heritability of Intellectual Quotient) – equine and human genetics are comparable. However, are they enough to explain the strong observed correlations between relatives in the Thoroughbred population without including an element of true heredity? How can one distinguish between genetic heritability and what the human geneticists call 'cultural' heritability? Some authors (Schulze-Schleppinghoff et al, 1985; Hill, 1988; James, 1990) seem to favour the predominance of 'cultural' effects. Others, including ourselves in France and Gaffney and Cunningham (1988) in Ireland and, more recently, Chico et al (1989) in Spain and Preisinger et al (1990) in Germany, while not denying the factors likely to lead to overestimation, favour a significant degree of heritability in racing ability.

It must be borne in mind that Thoroughbreds do not race against the clock but against each other. For this reason in European countries, professionals place very little importance on speed achievements when selecting animals; very often, they are not even recorded. However, the few studies carried out on time performance (Dusek, 1965, 1977) show a strong relationship between this and race category. The higher grade the race, the faster the times. On the other hand, this criterion is only weakly heritable (Artz, 1961; Bormann, 1966; Langlois, 1975, 1978, 1980; Hintz, 1980; Tolley et al, 1985). Some exceptions can be encountered but they generally concern short distance races (Buttram et al, 1988; Moritsu et al, 1994). It is therefore not surprising that indirect selection for a trait with weak heritability should prove not very effective. All depends on the genetic correlation between the selection criteria and recorded speeds, and this has hardly been studied so far. However, Beatson (1989) showed that even if heritability and genetic correlation are strong, indirect selection on racing success criteria would hardly improve speed at all, because times achieved by horses in a race have a low variability.

The study of the Spanish Thoroughbred population (Chico and Langlois, 1990; Chico, 1994) shows that racing speed is not the best way to grasp Thoroughbred performance, its repeatability and heritability being virtually zero. On the other hand, criteria derived from ranking, prize money (constant relative decrease according to the rank, ie, the second horse receives half the prize money of the first, the third horse half of the second and so on) or speed corrected for race effect (within-race speed differential) very probably have a heritability of more than 0.10, a repeatability close to 0.25 and a genetic correlation between them of 1. These different criteria therefore express the same thing and are in effect different ways of grasping one and the same reality, ie, the ranking of the horses in the race, which is thus seen to be the essential criterion for evaluating Thoroughbred performance. This fully justifies the methodological approaches proposed by Tavernier (1989) for analysing this criterion. We would also point out that, with an average (n) of five races, the coefficient determination ($R^2 = nh^2/[1 + (n-1)r]$) of performance monitoring reaches 0.25 with a heritability (h^2) of 0.10 and a repeatability (r) close to 0.25, which would seem to more than justify a conventional genetic approach.

In conclusion, it appears that, in the present state of research findings, racing performance in Thoroughbred horses is moderately heritable, and is best expressed as the number of races won and ranks independently of performance against the clock. It is not surprising that, despite selection, time performance is improving very little, because no one is trying to improve it. This in no way implies that there is no real progress in Thoroughbred populations, consistent with the heritability ratings and the intensity of selection.

To the question asked in the introduction, we would answer: Yes, performance breeding is still effective in the Thoroughbred, but it no longer effects speed as such. It probably now affects only the physiological and psychological traits connected with racing effort. Racing effort can be defined as an abrupt shift from a submaximum speed to a maximum speed, for a brief moment. This sudden acceleration is prompted by challenges from other horses. It is commanded by the horse's psychological makeup and involves the mobilization of anaerobic muscular metabolism. The number of such efforts a horse can make during a race is limited and depends on its resistance and fighting spirit.

The pure breed: myth or reality?

International rules for initially registering horses in the Stud Book require eight generations of successive Thoroughbred x Thoroughbred matings, that is, no more than one part in 256 (4/1 000) of non-Thoroughbred blood. That is a very high degree of breed purity indeed! Introduction of foreign genes into the population is thus officially extremely limited. And this purity is further guaranteed by systematic parentage testing by blood typing tests which, since their introduction, have prevented any fraudulent input of non-Thoroughbred genes.

The pedigree of the horses can also be readily obtained five generations back, providing the subject matter for numerous dissertations. What have geneticists to say about this?

Identity control and management using blood markers makes the information that can be deduced from lineage extremely reliable. However, the amount of genetic information given by parentage diminishes rapidly with genealogical distance. A horse and one of its parents have half their genes in common: a horse and one of its grandparents have statistically one-fourth. The figure for three generations is one-eighth, and for n generations it is $(1/2)^n$. For $n = 8$, this is not far from zero. In practice, since only the phenotype is accessible, the coefficient of heritability of the traits being selected must be taken into account. This makes the figure converge towards zero twice as fast when heritability is 0.50 and three times as fast when heritability is 0.33. In all commonly found situations, therefore, a three-generation pedigree seems sufficient.

The advantage of knowing pedigrees is that it makes it possible to control inbreeding when selecting mating partners. In this connection, the work of Mahon and Cunningham (1982) and Galizzi-Vecchiotti (1977) on consanguinity in the Thoroughbred is of interest. The examination of pedigrees over five generations revealed a very low rate of consanguinity in Thoroughbreds, generally lower than 5%. However, analysis of blood markers reveals a far greater homogeneity in this breed than in others (Guérin and Mériaux, 1986). Is this due to a 'foundation stock effect'? Mahon and Cunningham (1982) explored the pedigrees of some brood mares back to the foundation mares and stallions of the breed and used a sampling technique to calculate their inbreeding coefficients. They found values ranging from 5 to 20%, which seems to indicate that knowledge of pedigree over five generations, which always gave very low ratings, did not adequately reflect the real situation. This phenomenon, which has also been described in the American Standardbred (Cothran et al, 1984), reflects the fact that there have been bottlenecks in the population at some time in the past, so that the genealogical tree widens out for the first few generations back but then narrows again, the distant ancestors proving to be always the same. If one discounts the mutations that may have occurred over the course of these many generations, this can lead, in practice, to very wide differences in the degree of consanguinity from one mating to another. However, this seems to be a very difficult problem to master: one would have to have reliable genealogical data going right back to the origins of the breed, and the means to process the data would require a very considerable computing capacity.

To conclude, the emphasis on breed purity does not seem to be necessary in genetic terms, especially in a structure where both parents are selected on the basis of their performance. It deprives the population of high-quality exogenous inputs and tends to reduce the available genetic variability by maintaining a certain diffuse consanguinity that cannot be mastered without considerable resources and data.

Inbreeding versus outbreeding

Whether to aim for consanguinity or to avoid it is a common topic of conversation when it comes to Thoroughbred breeding. Expressions such as "inbred 3 x 4 on Northern Dancer" have become a part of the jargon of the trade. This can be regarded as equivalent to a calculation of the consanguinity coefficient, ie, the probability, conditioned by the pedigree, that an individual will receive two identical allelic genes copied from one and the same gene in an ancestor.

When Thoroughbred breeding professionals discuss this matter, they generally refer to a fairly distant blood relationship that will only carry a weak probability of fixing the genes of the ancestor or ancestors in question. In addition, by this process, genes are arbitrarily fixed, whether or not the traits they carry are desirable. Independently of inbreeding depression, due to the loss of genetic variability at each locus, this practice also implies many failures in its chosen goal of concentrating in one individual as many favorable genes from illustrious ancestors as possible.

It can be said, therefore, that inbreeding at the rate that is usually practiced does not enable much gene fixing and, at the much higher rates that were practiced previously, it fixed genes arbitrarily, with too high a failure rate to be recommended in a species like the horse, which has a long generation interval and a high cost per animal. The only recommendation one can make is to avoid the practice of inbreeding, even though it still fascinates breeders at a subconscious level.

Respective roles of dam and sire

It was in Thoroughbred breeding that the notion of 'sire of dams' or 'damsire' first made its appearance, suggesting that it is not necessarily the same stallions that produce good race horses and good brood mares. Is this distinction well founded? And what is the reason for the importance laid on maternal origin in this livestock branch? Is it a mystical belief dating back to the dawn of time and the cult of the mother goddess? Is it due to lack of confidence in the paternal origin? Is it connected with variations in the ability of mares to bear and raise their offspring in simple terms of high growth rates and good health? Is the training effect confused with a maternal effect? Is there a cytoplasmic heredity factor, ie, genetic information that can only come from the dam? It could also stem from a selection recommendation. Knowing that stallions are highly selected, it may be assumed that on this side genetic variability is low; but on the dam side, variability may be assumed to be greater because dams have been bred less intensively. In which case it is recommended to pay greater attention to the choice of dam.

What can one conclude in the present state of knowledge? The first question to ask is: can one really demonstrate a difference between the paternal and maternal pathways of hereditary transmission in Thoroughbred breeding? The second question is, if such a difference does exist, what are the simplest hypotheses to account for it?

The answer to the first question is yes. As Langlois and Chico (1989) have shown, there is a clear difference (table I) between the two parental transmission pathways, in favour of the maternal pathway. The same

Table I. Illustration of the general asymetry of the paternal and maternal paths of heredity in racing horses.

Flat races [a]

	Log of earnings [1]			*Log of earning per placing* [1]		
	2 years	*3 years*	*4 years*	*2 years*	*3 years*	*4 years*
Paternal path b°/s.m [2]	0.12 ± 0.02	0.13 ± 0.01	0.07 ± 0.03	0.16 ± 0.02	0.16 ± 0.01	0.10 ± 0.02
Maternal path b°/m.s [2]	0.13 ± 0.02	0.17 ± 0.01	0.12 ± 0.03	0.22 ± 0.02	0.23 ± 0.01	0.20 ± 0.02

Trotting races [b]

	Log of earning [1]			*Log of earning per start* [1]		
	2 years	*3 years*	*4 years*	*2 years*	*3 years*	*4 years*
Paternal path b°/s.m [2]	0.05 ± 0.03	0.07 ± 0.01	0.12 ± 0.01	0.08 ± 0.03	0.13 ± 0.01	0.14 ± 0.01
Maternal path b°/m.s [2]	0.11 ± 0.03	0.11 ± 0.01	0.10 ± 0.01	0.18 ± 0.03	0.16 ± 0.01	0.15 ± 0.09

[1] Pre-corrected data; [2] partial regression coefficients; b°/s.m offspring on sire with constant mare. b°/m.s offspring on mare with constant sire. [a] According to Langlois and Chico (1989); [b] according to Langlois (1984).

situation can also be observed in trotters (Langlois,1984).

It is harder to give a conclusive answer to the second question. Perhaps, as Schulze-Schleppinghoff et al (1987) and Preisinger et al (1990) seem to assume, the most important environmental effects are trainer effects. It is noteworthy, however, that the trainers seek out products of the same origin and attach great importance to the maternal lineage. A great part of the environmental effects allowed to the horses will thus follow the genetic effects, and the greater the importance placed on the maternal origins, the more this will be so on the female side. As a result, belief in the importance of the female line would be self-sustained. But this does not solve the problem of where this belief came from; it doubtless originated from some actual phenomenon. In our opinion, it arose from 'maternal-breeder' effects, borrowing an expression from Tavernier (1987, 1988), ie, confusion between a 'breeder effect', always confused with the brood mare effect, and the effect of variable mothering ability that will make a mare more or less capable of bearing, suckling and raising her foal, independently of the foal's genetic racing potential.

During the 48 months of a Thoroughbred foal's growth, the most decisive stage is the first third: the period of gestation and suckling, and this, of course, depends entirely on the dam. This stage has a very strong impact on the foal's final development. Therefore, the mother's contribution is indeed not restricted to her genetic input but includes part of the environmental influence: the part that depends on the maternal environment she provides. Knowing that these traits are themselves heritable, they justify the notion of a damsire and can explain the apparent asymmetry between the paternal and maternal pathways of heredity.

Finer phenomena such as cytoplasmic heredity or genomic imprinting (which means that only the alleles from the sire or only those from the dam are expressed in the early stages of development of some tissue or other in the embryo and therefore strongly influences the adult) are partly taken into account in modelling the maternal effect. Integrating these phenomena into more detailed models will be an interesting research prospect but, for the time being, there is no evidence suggesting that they are significant.

PROSPECTS

The economics of Thoroughbred production is dominated by speculation on breeding stock and depends to a much lesser extent on the levies on bets that provide the prize money. The industry therefore depends on the postulate that heredity is of prime importance. And as breeding value is difficult to establish clearly, this leads to a kind of poker game on a large scale, in which the operators have no interest in openness or visibility. One should also take into account the national versus international aspect of this industry and not neglect certain purely technical aspects that could in the future make breeding methods backfire disastrously. The shrinking of a national population's gene pool is a problem often mentioned. No one knows the situation in this regard at present. Independently of the usual economic operators, the national authorities ought to take an interest in the issue, to avoid a decline in this profitable branch of international trade.

It therefore seems important, first of all, to considerably improve the performance criteria used. Many statistical publications on gross prize money seem altogether outdated and ought to be improved. The techniques for doing so have long been available, are widely used in the saddle horse industry and are now also being applied to trotters. The new techniques could themselves be improved by using ranks rather than prize money, together with the system developed by Tavernier (1989, 1990, 1991).

A second stage would be to establish precisely the degree of heritability of racing performance in the Thoroughbred. There is much debate on this subject in scientific circles, and the facts must be definitively established. The credibility of present economic practices depends on it. Why should one pay more for this or that pedigree or high-performing sire if performance is not heritable? It would be nonsense. However, this problem is already largely solved. According to Preisinger et al (1990) and Schulze-Schleppinghoff et al (1987), it would seem that most of the hard-to-verify environmental effects are trainer effects. The German analyses take into account the trainer effect, and this considerably reduces heritability (table II). However, it must be stressed that, in these analyses, genetic effects and trainer effects are assumed to be independent. In other words, apart from statistical fluctuations, the genetic level of every trainer's foal batches is assumed to be the same as that of every other trainer. But this supposition does not seem to be justified. As a result, it seems that these analyses in fact provide a lower limit for heritability: at present, for annual total prize money, this is around 0.10.

The values we have obtained for the same variable, without correction for the trainer effect, are around 0.25 (Langlois and

Table II. Comparison of heritability values obtained in Germany taking into account the trainer effect or not.

Authors	Schulze-Schleppinghoff et al (1985) * Schulze-Schleppinghoff et al (1987)			Preisinger et al (1989) * Preisinger et al (1990)		
Criteria	*Handicap*			*Annual earning*	*Earning per race*	*Rank per race*
	2 years old	*3 years old*	*4 years old*			
Heritability without the trainer effect	0.22	0.35	0.38	–	0.26	0.32
	*0.22	*0.48	*0.52	*0.51	*0.13	*0.14
Heritability with the trainer effect	0.23	0.09	0.14	–	0.17	0.19
	*0.20	*0.20	*0.19	*0.11	*0.07	*0.07

* Last publication on the data.

Chico, 1989) and probably constitute an upper limit. Fine-tuning this approach is all that is required for drawing a definite conclusion on this issue.

As a third step, knowing the heritability ratings will enable us to move on to a genetic evaluation of Thoroughbreds. The BLUP animal model (Tavernier, 1987, 1988) seems particularly suitable since it incorporates a maternal effect and an environmental effect which is shared by all of a horse's performances and which therefore includes the trainer effect. Furthermore, because a horse is evaluated on the basis of its own performance and that of all its family, the BLUP animal model also corrects for the quality of the mates bred to each breeding animal. Independently of the evaluation of the animals, this procedure also makes it possible to assess genetic trend over recent decades.

There remains a need to pinpoint the racing success factors that are selected. With this in view, distance capacity will no doubt have to be studied more thoroughly. The emergence within the breed of more specialized lines such as sprinters, milers and stayers diverges from the principal objective, which is the production of the classic Thoroughbred, ie, a horse able to win on 2 400 m. This is one way of reintroducing an outbreeding logic into a purebreeding scheme, aimed only at eliminating from the breeding stock a large number of males and females, as accurately targeted as possible, so as to retain only the best to procreate the next generation. Whether mating is random or carried out very thoughtfully has little effect on the average quality of the next generation as a whole, but this is the major preoccupation of individual breeders. To advise the breeder on this issue, we shall therefore have to examine much more closely the different traits involved in racing success. What we can say is that analysing pedigree alone will provide no magic answer to this issue. The various mating systems suggested so far have no biological grounding and, whatever their protagonists may claim (Roman, 1984), their efficacy has in no way been proven.

CONCLUSION

From our examination of all these questions, it emerges that the genetic management of Thoroughbred populations could be greatly improved by using methods that research has already virtually perfected. Unfortunately, horse breeding is a very old-fashioned industry, convinced of the firm grounding of its archaic methods, and does not seem ready to adopt these proposals. The reason is doubtless that there are very few technical organizations responsible for coordinating horse breeding. Breeders regard their fellow breeders as competitors and can see no point in cooperating for genetic improvement. This restricts them to searching for the formula for some mythical, ideal mating that will give them the champion they hope one day to own. And with that approach, obviously, dreams count for more than reality.

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