SELECTION LIMITS IN THOROUGHBRED HORSES

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SUMMARY

It is well established that winning times in classic races for thoroughbreds have improved little, if at all, during this century, despite continued selection for racing success and apparently moderate to high heritability of performance. Actual heritability is almost certainly lower than appears, and it is not certain that performance and time are closely correlated. A positive estimate of genetic trend in performance may not be justified. It is conceivable that limited effective population size and intense selection have led to a plateau in performance, and the appearance of heritability of performance is illusory.

INTRODUCTION

Thoroughbred horses have long been subjected to performance tests, and selection has been based to a large extent on the results of these tests. It is therefore to be expected, on the assumption that performance has at least a non-negligible heritability, that genetic improvement in performance would have been achieved. Hamori and Halasz (1959) showed that although times for winners of "classic" races declined for many years, there has been little reduction in times during the 20th century. On the other hand, many studies, reviewed by Tolley et al. (1985), have indicated a moderate to high heritability for performance measured in various ways. Interest in the topic has been rekindled by the work of Gaffney and Cunningham (1988) and the commentary by Hill (1988). Gaffney and Cunningham used a BLUP procedure to estimate genetic trend in performance as 0.94 Timeform rating units per year. If there is genetic improvement being made, one must ask why times are not steadily improving. On the other hand, it is possible that a selection limit has been reached, since there are clear examples of such limits in laboratory populations, though these may sometimes be surpassed by the provision of new variation through spontaneous or induced mutation or through crossing. If no genetic improvement is being made, one must ask why heritabilities and genetic trends for performance have positive estimates.

CAUSES OF SELECTION LIMITS

A plateau in performance despite continued selection may have several causes:

1. Selection is not effective;
2. the environment is deteriorating;
3. natural selection opposes artificial selection;
4. additive genetic variance is exhausted.

The concept of a "physiological limit" is sometimes invoked to explain a lack of response to selection, but this is really another way of looking at lack of genetic variance. A physiological limit exists only if no genetic variation exists to permit "breaking through the barrier". The concept is used to imply that perhaps a very considerable genetic change is required. I do not find the concept helpful, since we cannot be certain if such a limit exists, or, if it does, whether it has been attained.

There seems no doubt that effective selection for some measures of performance is carried out, as shown recently by Gaffney and Cunningham, and previously by others. It is not so certain that selection is applied to times, and so far as I am aware there have been no published estimates of the genetic correlation between time and other performance measures. This is understandable, since data on times is rather limited, but such estimates could be useful. However, there seems no doubt that selection for performance was accompanied by improved times in the 19th century, though this was a phenotypic trend and not necessarily genetic. But it would be surprising if this trend had no genetic component.

The later lack of a phenotypic trend could be compatible with genetic improvement if the environment has worsened. It seems unlikely that veterinary and nutritional conditions have not improved this century, and, while training and riding methods may be traditional, it is hard to believe that they are poorer than they used to be, or that racing tracks have changed for the worse. Kimura (1958) showed that environmental deterioration could arise through improved competitive ability of other members of the population, which is akin to Fisher's remark that mean fitness will always be close to unity, an increase in fitness being manifested in a larger population. Since racing success is a matter of competition, rather than some external standard being applied, this mechanism may play some role. However, if an increase in speed occurred, it would fall outside this framework. It may be argued that in longer races the jockeys set a pace which they believe to be appropriate, and if they do this by reference to previous races of the same type they may exert a stabilising force tending to hold race times constant. Nevertheless, had large changes in horses' abilities occurred during this century it would be surprising if jockeys did not exploit these greater abilities.

A selection limit can be reached through a balance between natural and artificial selection, based either on a genetic relation between fitness and the selected trait (James, 1962) or on a model implying that genetically fitter animals tend to be intermediate for the selected trait (Verghese, 1974). Since fertility in thoroughbreds is notoriously troublesome, this may appear to be an attractive explanation. However, because of the large sums of money involved, special efforts are made to produce progeny from outstanding performers, so that even if they were less fit in a strictly biological sense (which has not been shown) it is likely that in practice they would have as many progeny as less outstanding animals. Langlois (1980) states that this is so for French mares. Since demand for matings is higher for outstanding stallions, they would contribute on average a large number of progeny to the next generation. While this does not preclude some natural selection against high performance through progeny viability, it seems unlikely that conflict between natural and artificial selection has produced a limit.

Therefore, if a limit has been reached, and additive genetic variance is present, none of these explanations seems convincing. We must therefore consider whether the estimates of positive genetic trend and substantial additive genetic variance may be misleading.

GENETIC TREND AND GENETIC VARIATION

Recognising that definite conclusions cannot be reached from phenotypic trends, Gaffney and Cunningham (1988) used a simple sire model BLUP analysis to estimate genetic trend in Timeform ratings as 0.94 units per year, compared with their predicted value, based on the same heritability of 0.36, of 0.92 units per year. This apparent genetic trend contrasted with a phenotypic trend of -0.32 units per year, which they attributed to the inclusion of a greater number of lowly rated horses in later years. This explanation indicates that horses used to supply data for analysis had been selected, violating the requirement for validity of BLUP analyses that all information used for making selection decisions should be used in the analysis. It is hard to predict the effect of this type of bias in the data. One possibility is that as more poor performers are included over time, the apparent breeding values of older sires would decline, giving the appearance of genetic improvement. On the other hand, younger sires may perhaps have a higher proportion of poorer progeny included in the data. The only clear conclusion is that the analysis of such data should be treated with great caution.

The agreement between the estimated trend and the predicted response is fortuitous. The selection differential reported for sires is based on selection from among colts only, but geldings should be included in the calculation, because the operation of gelding represents a selection decision. Since geldings on average perform considerably worse than colts, the actual selection differential, and hence predicted gain, would be larger than given by Gaffney and Cunningham, unless a lower heritability is appropriate. Thompson (1986) has shown that in some circumstances estimated values of response are extremely sensitive to assumed heritabilities. However, Gaffney and Cunningham reported that a one - third increase in assumed heritability produced only a 5 % increase in estimated response, so their results may not be extremely sensitive to assumed heritability. It would be interesting to know the effect of a very low assumed heritability. Tolley et al. (1985) reviewed estimates of heritability for earnings [19 estimates, unweighted mean 0.26], handicap [48, 0.54] and time [19, 0.21]. These values suggest all traits are moderately heritable, but it is widely recognised that such estimates are often liable to upward bias through assortative mating and correlation between genotype and environment. Despite efforts to allow for such effects, it is likely that the heritability used by Gaffney and Cunningham is too high and that they have over-estimated the genetic progress.

Even if performance as measured by Timeform rating is genetically improving, the genetic correlation between time and winning ability may not be high, so that given the lower heritability for time, correlated improvement in winning times might be small. It is difficult to imagine that it would be so small as to be undetectable over 50 years if substantial progress were being made in racing ability. Another factor to be considered is that ratings are based on results of races over various distances, so that if genetic progress occurs in short race performance this could result in improved ratings even if there is no improvement in long race performance. This could be analogous to part-record selection in laying hens, where genetic gains were made in part-record production while no gains were made in full-record production (Morris, 1963). Racing success is not a single trait, and the rating can be viewed as an index of several traits.

For several reasons, then, Gaffney and Cunningham's results may be compatible with exhaustion of additive genetic variance for performance in longer races. This would not necessarily imply that selection within the population is worthless. Epistatic variance of the additive by additive type contributes to the resemblance of parent and offspring, and Griffing (1960) showed that selection can use such variation, building up favourable gene combinations through linkage disequilibrium. If selection is discontinued, recombination will randomise the gene combinations and the mean performance will decline. Thus, although no further improvement is made, selection is successful in that better parents produce on average better progeny, and if selection is suspended the average performance of the population will deteriorate.

DISCUSSION

We are left without a firm conclusion. The phenotypic stability may or may not reflect a genetic stability, since the only real attempt to estimate genetic trend is subject to very strong reservations. The apparent existence of additive genetic variance is also of doubtful validity. Given the large sums of money involved in breeding thoroughbred horses, it seems worthwhile that more thorough investigations should be made, despite the difficulty in obtaining suitable data.

If, despite all the efforts made, thoroughbreds are no longer improving, it is perhaps time to seek new methods. In a laboratory population an outcross would be the obvious first suggestion, provided that a suitable source of animals were available. It may be that other horse breeds would be too uncompetitive for early success in crosses with thoroughbreds, but this cannot be known if not tried. It may be asked whether the breed has become differentiated among different countries around the world, so that systematic crossing of animals from different places could be undertaken, recognising that considerable migration does occur in an unsystematic manner.

On the other hand, if genetic gains are still being made, why are race times not improving? Is it that trainers and jockeys are unable to adapt their methods to take advantage of the genetic improvement? No matter which way we try to resolve the puzzle, we are led to the conclusion that something needs to be done, either to improve the horses or to improve those who deal with them, unless we accept that since horse racing is a matter of competition the only thing that matters is that differences should exist, no matter what their nature may be.

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