Is selection on semen characteristics needed ?

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Abstract

A.I. studs and selection programs are interested in the broad distribution of sires of high genetic merit. This is at least partly conditioned by the semen characteristics (sperm quality and volume of the ejaculates) of the bulls. However, when most bulls have a satisfactory production or when management can be optimized to ensure maximum output, selection on semen characteristics can be considered too costly.

In the last two decades, 10 to 15% of young Normande bulls have been culled each year due to their poor sperm quality. This selection had virtually no impact on their semen production. Nevertheless, it was found that selection was practiced correctly and that the traits selected are heritable. These contradictory results can be explained by the unfavorable influence in the breed of some heavily used sires of bulls with a poor genetic merit on sperm production traits.

If the objective is to avoid a significant degradation of semen quality, one may conclude that a careful monitoring of the bull population is required. A proper genetic evaluation using all the information available (BLUP-animal model) must be implemented routinely. Then, efficient selection can be practiced if needed, at least within the families with the most unfavorable genetic characteristics.

1. Introduction

An obvious objective of A.I. studs is the broad distribution of semen from the best bulls at the lowest possible cost. Evidently, this has favorable consequences on profit for A.I. studs and on genetic progress for the important traits in the whole population. But to achieve such a goal, any adult sire should be able to produce a large number of doses with good fertility.

Male fertility can be assessed precisely by analyzing fertility measures such as non-return rate (Stalhammar et al, 1997; Boichard et al, 1997) or indirectly, by studying one of its components: semen quality. The relationship between semen quality and fertility is still not very well known, in particular because semen batch identification is rarely available (this is needed to relate the result of one insemination to semen characteristics of the corresponding ejaculate) and because many environmental factors strongly affect fertility and must be corrected for, before reliable conclusions can be drawn. Nevertheless, semen characteristics are always considered in the stud: semen quality is usually described through indicators such as sperm motility, sperm concentration, fraction of motile spermatozoa before or after thawing, or percentage of abnormal spermatozoa. Combined with the volume of the ejaculate, semen quality conditions the total number of doses that can be made from one ejaculate.

Sperm production and quality are influenced by a variety of management, environmental and genetic factors. For example, they increase with the age of the bull (Cunningham et al, 1977; Taylor et al, 1985; Mathevon et al, 1997ab). They also vary with sexual preparation (Signoret, 1962; Almquist, 1973; Mathevon et al, 1997a), with season of collection (Everett et al., 1978), with number of ejaculates collected and interval between collections (Cunningham et al, 1977; Mathevon et al, 1997a,b).

Still, heritability of semen characteristics has been found to be moderate to high (Stalhammar et al, 1989; Ducrocq and Humblot, 1995; Mathevon et al, 1997a,b).For this reason, selection programs have been running for a long time (since 1974 in the Normande breed) with a systematic evaluation of semen characteristics in test stations on young bulls, usually after performance test on growth (Figure 1, Thibier and Colchen Bourlaud, 1972). The efficiency of such a selection in the Normande breed, for which 10 to 15% of young bulls were culled each year on the basis of early sperm production (Parez and Thibier, 1983; Thibier, 1991) has been questioned. This paper reviews the results obtained in two studies (Humblot et al, 1993; Ducrocq and Humblot, 1995) which try to analyze the efficiency and the interest lying in the selection practiced.

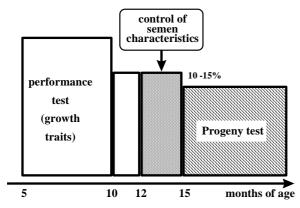


Figure 1. Description of selection steps for young bulls in the Normande breed.

2. Selection on semen characteristics in the Normande breed.

After performance test on growth and a month of adaptation, young Normande bulls were tested for semen production between 12 and 15 months of age, at a unique location («Génétique Normande Avenir », L'Aigle, France) and under the supervision of the same technician over the whole period under study (January 1975 - December 1986). During this period, the average volume of the ejaculate, the average motility score (on a subjective scale from 0 to 4), the average sperm concentration and the average percentage of motile sperms after thawing were obtained for 2454 bulls (after some editing), based on 11.4 \pm 3.6 samples per bull, each of two successive ejaculates. Data on total percentage of abnormal spermatozoa were also available on a subset of these ejaculates but are not considered here (see Ducrocq and Humblot, 1995). At the end of the test, a final subjective score was given by the technician, summarizing the semen production of each bull. This score defined 5 groups : « very good », « good », « fair », « culled at the end of test », « culled during the test ».

The selection applied led to the elimination of 13.6% of the bulls based on semen characteristics.

This corresponds to a selection intensity of 0.252, or an expected response of 0.063 genetic standard

deviation per generation when selection is applied to only one trait with an heritability of 25%.

Unfortunately, there was no observed response to the mass selection performed, even when the low selection intensity is considered. Figure 2 presents the yearly phenotypic and genetic means for motility score (for the other traits, see Ducrocq and Humblot, 1995). Breeding values were estimated using parameters obtained from the data set. For all traits considered, the genetic trend is either null or slightly negative (e.g., -0.07, +0.02, -0.19, +0.07 genetic standard deviation over 11 years for volume, motility, concentration and motile spermatozoa after thawing).

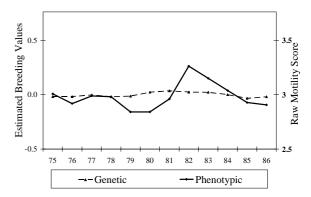


Figure 2. Phenotypic and genetic trends for motility score (same scale for both vertical axes = 2 phenotypic standard deviations)

3. Why was selection inefficient ?

This obvious lack of efficiency of the selection practiced has to be explained. Several hypotheses were studied :

3.1. The final score given by the technician at the end of the test may be meaningless

A first interpretation is that the final score given by the technician and on which culling is based incorrectly reflects differences in semen quality between bulls. Table 1 presents the mean value

Table 1. Raw mean values of semen characteristics in the groups determined by the technician during test in station

Groups (number of bulls)	Culled during Culled at the test end of test		Fair Good		Very Good		
× ,	(62)	(271)	(241)	(1464)	(416)		
Volume (ml)	2.69	3.08	3.00	2.91	3.71		
Motility Score (0-4)	1.57	1.82	2.73	3.17	3.43		
Concentration $(10^9/ml)$	0.53	0.66	0.87	1.00	1.20		
Motile Spermatozoa	-	7.43	14.5	24.4	29.6		
after thawing (%)							
Doses /ejaculate ^(a)	-	16.4	37.4	68.5	127.5		

(a) theoretical number combining volume, concentration and motile spermatozoa after thawing

of the semen characteristics in station for each group defined by the technician. Obviously, huge differences do exist between groups for the three semen quality indicators. On the other hand, volume only discriminates the « very good » bulls from the others. If the main elementary variables (concentration, motile spermatozoa after thawing and volume of the ejaculate) are combined to calculate a theoretical number of doses per ejaculate, each group produces approximately twice the number of doses of the immediately inferior one !

3.2 Performances recorded on young bulls in station may be different from performances of adult bulls.

The ability to characterize the semen production of an adult bull using its first few ejaculates when the bull is 12 months old can be questioned : they may be too variable to actually be used for selection purposes, or they may be related to completely different characteristics (precocity).

In fact, in 2 of the 6 A.I. studs testing Normande bulls coming out of the « Génétique Normande Avenir » program, it was possible to study the relationship between the early measures recorded in station and later semen characteristics and production. In these studs, semen was collected for all bulls until 50,000 doses were available, then collection was stopped until the progeny test results were known. Only the first 3 years of data were used in the analysis, as collection in year 4 and later was continued only if the bull was a bad producer. For a total of 409 bulls over the period 1976-1988, trimestrial (for the first year) and annual means (for years 2 and 3) were calculated from monthly values.

The analysis consisted of (see Humblot et al, 1993 for details):

• a correction of semen traits measured in station for environmental and management effects;

Table 2. Correlations between estimated bull effects for two periods of production in the studs and the corresponding corrected performances in stations

	Year of production						
Trait	1	2 and 3					
Volume	0.70***	0.57***					
Motility score	0.28***	0.15 **					
Concentration	0.57***	0.43***					
Doses / month	0.35***	0.21***					
**: p<0.01							

- a best linear unbiased estimation of a (random) bull effect in the stud during the first and later years, treating trimestrial and annual means as repeated measures and correcting for environmental and management effects;
- a comparison of the predictions of bull effects of the two periods (year 1 vs 2 and 3) and of the corresponding corrected performances in station (Table 2);
- a comparison of semen characteristics in the studs of bulls classified in different groups by the technician in station(Figure 3).

For all the traits, bull effects computed separately for the first and later years were highly correlated (0.57 to 0.79), indicating relatively little variation in the adult bull's ability to produce semen. The relationship between station and AI studs performances was quite high for volume and concentration and moderate for the other traits, with a decrease in the correlation as the bulls get older. However, it is important to notice that these correlations are likely to underestimate the true ones, because :

- bulls with undesirable semen characteristics were culled before entering the studs;
- the correlations were calculated using bull effects estimates, without accounting for their limited accuracy;
- the correction for environmental and management effects was applied to average performances. When data are recorded and analyzed separately for each ejaculate (as it is the case now), correction is more precise than for average values (Mathevon et al, 1997ab);

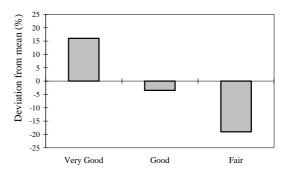


Figure 3. Semen production during the first year in the stud according to the classification given by the technician in station

Furthermore, Figure 3 clearly shows that substantial differences in semen output are observed between extreme groups, as classified by the technician (see Humblot et al, 1993, for the other variables). Therefore, the representativity of the early performances is satisfactory, even though it is not perfect, and tends to get diluted as time goes.

3.3. The traits considered may be difficult to select

This would be the case if their heritability is low, or if they were negatively correlated and all included as selection criteria.

Genetic parameters were estimated by Restricted Maximum Likelihood (Patterson and Thompson, 1971) using a subset of 1957 bulls born after January 1976. An animal model was assumed. The whole analysis is described in Ducrocq and Humblot (1995). The main results are presented in Table 3 : the volume of the ejaculate is highly heritable (0.65)and opposed to the three sperm quality traits which are all moderately heritable and strongly correlated. The heritability values were higher than those usually found in the literature but this is easily explained by the fact that the traits analyzed are averages of a relatively high number (11.4) of repeated measures. A full Bayesian analysis was also conducted using the exact same data set (Hofer and Ducrocq, 1997). It clearly confirmed the previous conclusions, with the extra benefit of having the full marginal posterior distributions of heritabilities and correlations instead of just point estimates.

Table 3. Heritabilities (on the diagonal), genetic (above the diagonal) and phenotypic (below the diagonal) correlations between traits

	Trait			
Trait	1	2	3	4
1-Volume	0.65	-0.17	-0.43	-0.26
2-Motility score	0.02	0.23	0.67	0.81
3- Concentration	-0.11	0.65	0.37	0.55
4-Motile spermatozoa	-0.03	0.77	0.54	0.24
after thawing				

Table 4 presents the average breeding values of the selected bulls, as well as the genetic characteristics of each group defined by the technician. As

suspected given the results reported in Table 1, the technician's classification reflects genetic differences in semen quality traits consistently. Selection was not applied on all traits identically : selection was more intense on motility score, followed by concentration and fraction of motile spermatozoa after thawing. Volume received just enough emphasis to avoid the expected degradation corresponding to the correlated response to selection on quality traits. Overall, it can be concluded that selection was done properly, focusing on the 3 correlated quality traits with a reasonable heritability.

3.4. Mass selection may hide an underlying genetic drift

Selection on own performance was done within contemporary group. One characteristic of the Normande breed has been the high selection intensity of bull sires. Indeed, only 5 to 8 progeny tested bulls were used each year to produce the next generation of young sires. These bulls were often closely related (e.g., half sibs) and used in a very unbalanced way. It was checked that the resulting increase in inbreeding coefficient does not explain the absence of response to selection on semen characteristics (see Ducrocq and Humblot, 1995).

As a consequence, many contemporary groups included a reduced number of half sibs groups. In the Normande breed, two bulls, Nick and his son Valhalla, had an extreme influence due to their high genetic merit on dairy traits. Their contribution is illustrated in Figure 4 : at the end of the seventies, a significant number of performance tested bulls were progeny or grand-progeny of these bulls. Later, quite a few sires of bulls were sons of Valhalla, providing 2/3 to 3/4 of the young bulls tested in the 1984-1986 period.

For sperm characteristics, the estimated breeding values (EBVs) of Nick and Valhalla based on their numerous sons and grand-sons were poor (e.g., for Valhalla : volume : -1.17 genetic standard deviation, motility : -0.94, concentration : -1.14 and motile spermatozoa after thawing : -0.85 !).

Table 4. Average breeding values (in genetic standard deviation) for semen characteristics in the groups determined by the technician during test in station and for selected bulls.

Groups (number of bulls)	Culled during test	Culled at the end of test	Fair	Good	Very Good	Superiority of selected bulls ^(a)
Volume	-0.07	0.10	-0.01	-0.13	0.36	-0.01
Motility Score	-1.04	-0.78	-0.25	0.11	0.32	0.13
Concentration	-0.54	-0.49	-0.20	0.05	0.27	0.08
Motile Spermatozoa	-1.03	-0.40	-0.36	0.11	0.32	0.08
after thawing						

(a) compared to all candidates to selection

	Bull (number of tested sons)									
Characteristic	Nuez	(67)	Mazolla	(85)	Newgate	(89)	Outremer	(76)	Mètre	(76)
Volume (ml)	3.20	2.97	2.45	2.99	3.25	3.10	2.60	3.40	2.95	3.14
$(EBV)^{(a)}$	(-0.51)		(-0.56)		(0.42)		(-0.56)		(0.24)	
Motility Score (0-4)	3.15	3.00	3.60	3.21	2.75	2.93	2.50	2.71	2.20	2.96
(EBV)	(0.05)		(0.87)		(-0.74)		(-1.08)		(-0.97)	
Concentration $(10^9/ml)$	1.20	1.01	1.26	0.94	0.87	0.85	0.64	0.75	0.74	0.86
(EBV)	(0.99)		(0.31)		(-0.88)		(-1.55)		(-0.93)	
Motile Sperm. (%) ^(b)	33.5	21.5	30.5	22.7	21.0	21.1	18.0	18.1	12.0	21.3
(EBV)	(0.29)		(0.68)		(-0.36)		(-0.96)		(-0.59)	

Table 5. Phenotypic characteristics of 5 sons of Valhalla (first column) and of theirs sons (second column).

(a) Estimated breeding value of the bull, in genetic standard deviation

(b) After thawing

The average performance of the contemporary groups reflects the genetic merit of the sires used only in part. Within group selection completely hides the possibility of a genetic drift in the population when a few extreme sires of bulls are used. This is confirmed when the contributions of the sons and grand-sons of Nick and Valhalla are separated from those of the other bulls (Figure 5a,b, see Ducrocq and Humblot, 1995, for the other traits) : the progeny of Nick and Valhalla are consistently and significantly poorer than the other bulls. In contrast with the conclusion drawn from Figure 1, a slight, significant progress in motility score is observed for bulls not closely related to Nick and Valhalla.

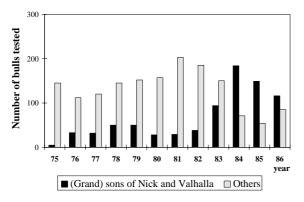
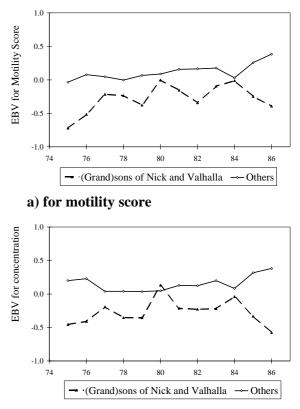


Figure 4. Number of sons and grand-sons of the bulls 'Nick' and 'Valhalla' which were performance tested for semen characteristics.

Finally, Table 5 illustrates the existing variability on sperm characteristics, even within « poor » families : Among the 5 sons of Valhalla that were the most heavily used as sires of bulls, 2 had reasonably good own performances (Nuez and Mazolla) while the other 3 were unsatisfactory. This ranking is clearly the same for the raw performances of their progeny, as well as for their own estimated breeding values: knowing the poor merit of Valhalla, it would have been possible to increase the selection intensity on semen characteristics among his sons in order to limit his negative contribution more efficiently.



b) for concentration

Figure 5. Average genetic merit of sons and grand-sons of 'Nick' and 'Valhalla' and of other bulls

4. Conclusion

This study was carried out to understand why no clear genetic trend for semen characteristics was detected in the Normande breed. Selection appears to have been performed correctly, on moderately heritable traits. Indeed, the selection practiced may have prevented a decline in average genetic merit for semen quality, due to the heavy use of some sires of bulls with detrimental characteristics.

Selection would have certainly been more efficient if applied to the results of a genetic evaluation using all the information available, i.e., using BLUP EBVs based on an animal model, as was done here. The implementation of such an evaluation allows a precise description of the genetic evolution of the whole population : when by chance the sires of bulls have satisfactory EBVs, selection pressure on semen characteristics can be relaxed. Conversely, an unfavorable trend can be avoided through more severe culling in the worst families.

These considerations can be extended to other traits whose economic weight is small but for which an important degradation must be strictly avoided: one has to be aware that the very high selection intensities applied on the main traits may lead to unpredictable evolution of these secondary traits. A careful monitoring of the population is required, through regular data collection and proper genetic evaluations, in order to apply selection if necessary.

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