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Factors affecting commercial application of embryo technologies in dairy cattle in Europe—a modelling approach

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Abstract

Reproductive techniques have a major impact on the structure of breeding programmes, the rate of genetic gain and dissemination of genetic gain in populations. This manuscript reviews the impact of reproductive technologies on the underlying components of genetic gain and inbreeding with special reference to the role of female reproductive technology. Evaluation of alternative breeding schemes should be based on genetic gain while constraining inbreeding. Optimum breeding schemes can be characterised by: decreased importance of sib information; increased accuracy at the expense of intensity; and a factorial mating strategy. If large-scale embryo cloning becomes feasible, this will have a small impact on the rate of genetic gain but will have a large impact on the structure of breeding programmes.

Keywords: Genetic gain; Inbreeding; Embryo technologies

1. Introduction

Breeding schemes aim at utilisation of the between- and within-breed genetic diversity. Breeding schemes are not aiming at a fixed target; breeding organisations are dynamically searching for improvements. Differences in economic, social and ecological production environments give rise to different desired directions of change. The desired direction of change of a particular breed might differ between regions and change over time. Such changes over time are strongly driven by consumer and society. Breeding organisations are increasingly aware of this and are changing their breeding objectives by including traits related to animal welfare and quality of product. Reproductive techniques play an

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important role in the activities of the breeding organisation. In essence, the most basic effect of reproductive technologies is to increase fecundity. This means that fewer parents are needed to produce a given number of offspring. The application of reproductive techniques has had a major impact on the structure of breeding programmes, the rate of genetic gain and the dissemination of genetic gain in livestock production and aquaculture. Research on application of reproductive technologies initially focused on genetic gain while little attention was paid to inbreeding (i.e. longer-term consequences of selection for genetic diversity). However, it is now well accepted that an evaluation of alternative breeding schemes should be based on genetic gain while constraining inbreeding.

The objective of this manuscript is to review the impact of reproductive technologies on genetic gain and inbreeding in dairy cattle. The underlying principles will be described and illustrated. In addition, prospects for application of reproductive technologies are described. Subsequently, economic considerations for breeding organisations and farmers that influence the application of reproductive technologies are given from a European perspective.

2. Structure of livestock populations

Two activities need to be distinguished in breeding programmes. The first is the generation of genetic improvement by selecting animals based on their estimated breeding value for the relevant traits. Secondly, there is the dissemination of superior genetic material from the nucleus to the commercial population. The genetic improvement is generated in a small fraction of the population (referred to as nucleus animals). In pigs and poultry, closed nucleus schemes are generally used in which nucleus animals are kept on a small number of farms and only animals from these nucleus farms can contribute to genetic improvement of the nucleus population. In dairy cattle, open nucleus schemes are used, i.e. commercial and nucleus cows are eligible for selection as parents for the next generation of nucleus animals.

In pigs and poultry, a typical breeding programme involves a number of sire and dam lines. Increasingly, nucleus breeding stock of these lines is centrally owned by breeding companies [1], producing crossbred breeding stock for commercial producers. In contrast to the dairy cattle situation, nucleus breeding stock is not used for commercial production. From a genetic point of view there are three reasons for the use of crossbreeding in pigs and poultry, namely (1) female reproductive rate, (2) heterosis for relevant traits and (3) the possibility of combining specialised lines to meet the demand in different markets. Breeding companies can protect their ownership of elite genetic material by only selling crossbred breeding stock to commercial producers. Crossbreeding is hardly used in dairy cattle in Europe. In this industry, female breeding stock is typically farmer owned but there are a number of breeding companies that also own breeding females.

3. Rate of genetic gain

The rate of genetic gain (ΔG) in a population under truncation selection can be predicted based on the intensity of selection (i), accuracy of selection (ρ), additive genetic standard

deviation (σ_A) and generation interval (L) in the different paths of selection (j) [2]:

$$\Delta G = \frac{\sum i_j \rho_j \sigma_{Aj}}{\sum L_j}$$

This expression holds for quantitative traits, i.e. phenotypes for the traits are influenced by genetic factors and environmental factors. The infinitesimal model, which assumes that traits are the result of a very large (effectively infinite) number of loci with a very small (infinitesimal) effect, is assumed for the genetic factor [3]. Under this model, breeding values follow a normal distribution and traits behave linearly.

3.1. Genetic variance

The genetic variance in selection candidates is equal to:

$$\sigma^2_{Ai} = \tfrac{1}{4}\sigma^2_{As} + \tfrac{1}{4}\sigma^2_{Ad} + \sigma^2_{Am}$$

where σ^2_{Ax} is the genetic variance in the selected sires ($x = \mathrm{s}$) and dams ($x = \mathrm{d}$) and σ^2_{Am} is the Mendelian sampling variance. In an unselected and non-inbred population $\sigma^2_{As} = \sigma^2_{Ad} = \sigma^2_{Ai}$ and $\sigma^2_{Am} = 1/2\sigma^2_{Ai}$, which means that sires and dams each contribute 25% to the genetic variance in an individual and that 50% of the genetic variance is due to Mendelian sampling. Selection, however, results in a reduction of the genetic variance in the selected parents, the so-called Bulmer effect. The reduction in genetic variance in sires (dams) depends on the accuracy of selection and variance reduction coefficient which is a direct function of the selected proportion [3]. The genetic variance in the selected parents (x) is equal to:

$$\sigma^2_{Ax} = \sigma^2_{A}(1 - k_x \rho^2_x)$$

where k_x is the variance reduction coefficient, which is close to 0.8 in most cases, and ρ_x is the accuracy of selection.

The Bulmer effect leads to a reduction in genetic gain because the genetic gain is a direct function of the genetic variance. The variance reduction in the population is often close to 25%, which leads to a 13% reduction in the absolute gain. More importantly, however, the Bulmer effect reduces the genetic variance in parents (the between-family variance) but not the Mendelian sampling variance (the within-family variance). As a consequence, full- and half-sib information has become less important whereas information that includes the Mendelian sampling component of the selection candidate, such as own performance and progeny information, becomes relatively more important. These effects are important when assessing the rate of genetic gain of schemes that use different sources of information (e.g. progeny versus sib information).

3.2. Accuracy of selection

The accuracy of selection is the correlation between the selection criteria and the true breeding value for the breeding goal that is to be improved. Selection index theory can be used to calculate the accuracy of selection on the breeding goal. In most livestock

improvement schemes, selection is based on breeding values that are estimated using best linear unbiased prediction (BLUP). BLUP utilises the phenotypic information on all traits and relatives to predict the breeding values (EBV). A method for calculating the accuracy of selection on BLUP-EBV was developed by Wray and Hill [4]. A multiple-trait extension of this method was presented by Villanueva et al. [5] and Bijma et al. [6] with an extension for overlapping generations. These methods account for the reduction of genetic variance due to selection.

3.3. Selection intensity

In predicting the response to selection, it is generally assumed that the selection criterion is normally distributed and that truncation selection is applied. In that case, the selection intensity can be obtained directly from the proportion of animals that is selected. When the selection criterion is partly based on family information, the EBVs of sibs are correlated. Meuwissen [7] developed a method to account for finite population and correlated EBV. This correction is particularly important in breeding schemes that rely heavily on information coming from full- and half-sibs and where the number of selected parents is small.

3.4. Overlapping generations

In most populations, a number of age classes can be distinguished and the amount of information differs between classes. In general, young age classes have less information than older age classes. Because older age classes have more information, they have higher accuracy. However, the mean level of the EBV of older age classes will be lower than that of younger age classes due to the continuous genetic improvement in the population. Truncation selection across age classes can be performed to obtain the highest selection differential [8]. Mathematical details on truncation across age classes are described by Ducrocq and Quaas [9] and Bijma et al. [6]. The fraction selected from each age class depends on the differences in accuracy between age classes. Reproductive techniques might increase the amount of sib information and thereby increase the accuracy of EBV of younger age classes. This will change the fraction of parents selected from the younger age classes and, therefore, also influence the average generation interval.

4. Rate of inbreeding

The magnitude of inbreeding at the population level is measured by the rate of inbreeding (ΔF). Only in the absence of selection is ΔF related directly to the number of sires and dams. In selected populations, this equation is no longer valid because parents contribute unequally to the next generation. Wray and Thompson [10] introduced methods to predict rates of inbreeding in selected populations, based on the concept of long-term genetic contributions. Recently, Woolliams et al. [11] and Woolliams and Bijma [12] developed a general theory to predict rates of inbreeding in populations undergoing selection. These methods facilitate a deterministic optimisation of short- and long-term

response of breeding schemes. Bijma and Woolliams [13] demonstrated that with BLUP selection, the number of candidates per parent (selection intensity) may be as important, or more important, than the number of parents. Doubling the number of parents failed to halve the rate of inbreeding.

Meuwissen [14] introduced a dynamic selection tool to maximise the genetic gain while restricting the rate of inbreeding. Given the available selection candidates, the method maximised the genetic level of the selected group of parents while constraining the average coefficient of co-ancestry. Implementation of this method results in a dynamic breeding programme, where the number of parents and number of offspring per parent may vary, depending on the candidates available in a particular generation.

5. Optimisation of breeding schemes

Under the infinitesimal model, inbreeding reduces genetic variation, which in turn reduces genetic gain. Furthermore, when inbreeding depression is present, fitness of the population may reduce to an extent where it affects the selection differentials, i.e. indirectly inbreeding may also reduce genetic gain. In the short term, inbreeding and genetic gain have an unfavourable relationship, in the sense that maximising short-term response by selecting fewer parents reduces long-term response and involves substantial risk (e.g. [15]). To balance the short- and long-term responses, a restriction on the rate of inbreeding is required (e.g. [16]). The objective in optimised breeding strategies is to maximise genetic gain while restricting inbreeding. Acceptable levels of inbreeding are difficult to determine and are discussed by Bijma [17], who indicated that inbreeding depression is probably the most important issue. Though detailed knowledge of the relevant parameters to determine the level of the constraint is lacking, different approaches point towards values around 0.5 and 1% per generation.

6. Genetic lag

A key element in the dissemination of genetic material is the genetic lag, i.e. the difference in genetic merit between the nucleus and the commercial populations. Reproductive technologies can be used to improve the dissemination of genetic gain generated in the nucleus population to the commercial population and thereby reduce the genetic lag.

7. Impact of reproductive technology

7.1. Male reproduction

The first reproductive technique that had a major impact on animal breeding schemes was artificial insemination (AI). Rendel and Robertson [2] proposed the progeny-testing scheme to make efficient use of the possibilities offered by AI. Since then, progeny-testing schemes have been widely adopted in dairy cattle breeding, and many studies have been

directed at optimising the design of those schemes from a genetic and economic point of view. Although AI technology is still being improved and refined, breakthroughs in male reproductive technology with substantial consequences for breeding programmes or dissemination of genetic progress are no longer expected [18]. In the Nordic and Western European countries, AI use in dairy cattle is practically 100%.

7.2. Female reproduction

The production of the first calf by embryo transfer took place in March 1950 [19]. Considerable time elapsed between the first successful embryo transfer in cattle and the first large-scale applications which resulted from Cambridge research in the late 1960s (summarised in [20]). During the 1980s, multiple ovulation and embryo transfer (MOET) became increasingly feasible for use with cattle and resulted in increased reproductive rates of females. The main limitations of MOET are the low average and high variability of embryo numbers per female [21]. These limitations can be overcome to some degree by repeated non-surgical harvesting of ova from females (ovum pickup (OPU)), and subsequent in vitro maturation, in vitro fertilisation and in vitro culture which can yield large numbers of transferable embryos. This technology (referred to as in vitro embryo production (IVEP)) opens the way for a different mating scheme, called factorial mating, in which both females and males are mated to several members of the opposite sex [22].

A survey of IETS showed that 23,000 cows were flushed in Europe in year 2000, resulting in 125,000 embryos of transferable quality of which 106,000 were transferred [23]. Countries with the largest share in the production of transferable embryos were France (27%), Germany (19%) and The Netherlands (16%). No data was available on the United Kingdom for that year. In vitro production of bovine embryos resulted in 26,000 transferable embryos in year 2000 of which 14,000 were transferred [23].

7.3. Illustration of impacts of MOET in dairy cattle

An increase in reproductive rate of females offers the opportunity to reduce the number of dams that need to be selected for the next generation. At the same time, it leads to an increase in the amount of information available on sibs for estimating the EBV of male as well as female selection candidates. Among the early studies of the genetical implications of MOET were those by Land and Hill [24] for beef cattle and Nicholas [25] and Nicholas and Smith [26] for dairy cattle. The general conclusion from these studies was that MOET could produce substantial increases in genetic improvement. However, it was noted that the rate of inbreeding would also be substantially increased. Since the early studies, there has been a great deal of activity amongst quantitative geneticists to perform more sophisticated studies taking into account several important genetic phenomenon that were ignored in the initial calculations [21]. Today, it is clear that it is important to account for the Bulmer effect—the effect of correlated EBV on selection intensity and rate of inbreeding. The initial studies in particular underestimated the extent to which inbreeding would be increased and overestimated the value of information on sibs as compared to own and progeny information.

Table 1
Predicted rate of genetic response (ΔG) in genetic standard deviations (σ_A): contribution of selection in males to genetic response (% male) and rate of inbreeding (ΔF) for a breeding scheme[a] with different number of sires (N_s), number of dams (N_d) and female offspring per dam (N_o)

N_s	N_d	N_o	Percent male	Genetic response (ΔG)			
				ΔG			ΔF
64	64	2	38	1.58	−20%		0.5
32	64	2	50	1.97	–	100%	1.1
16	64	2	58	2.34	+19%		2.4
64	32	4	28	2.13	−19%		1.0
32	32	4	40	2.63	–	134%	2.0
16	32	4	47	2.97	+13%		3.9
64	16	8	24	2.60	−16%		1.9
32	16	8	35	3.09	–	157%	3.3
16	16	8	42	3.55	+15%		6.9

[a] Selection is for milk production measured on female selection candidates prior to selection only, with a heritability (h^2) of 0.25. The number of male selection candidates per female is N_o.

To illustrate the consequences of female reproductive rate, Table 1 gives predicted rates of genetic gain and inbreeding for breeding schemes with varying number of dams and sires. The number of offspring in all schemes is constant (i.e. 128 female offspring each generation) and predictions are based on truncation selection.

Increasing the number of offspring per dam from two to eight results in a 57% increases in genetic gain (ΔG). The change in rate of inbreeding (ΔF) is three times higher with eight offspring per dam as with two offspring per dam. Halving the number of sires has a moderate effect on ΔG (13–20%) while doubling ΔF. The effects of reducing the number of dams on ΔG are larger than for number of sires. This is due to the fact that the dam's own performance is used in predicting the EBV. The dam's own performance provides information on the Mendelian sampling term for the dam. Due to the Bulmer effects, the value of own performance information for predicting the EBV of selection candidates has increased whereas value of sib information has reduced. In addition, the dam's own performance causes a reduction in the correlation between EBV of selection candidates, which increases the selection intensity and reduces inbreeding.

7.4. Reducing the generation interval

In the earlier example, dams were selected after the recording of their production. Embryos can be collected at younger age resulting in a further reduction of the generation interval. Betteridge et al. [27] considered the IVEP of embryos from foetuses which can potentially reduce the generation interval in cows to 90 days. Meuwissen [28] predicted an increase in genetic gain of 13–18% resulting from IVEP of embryos from juveniles. However, rates of inbreeding will substantially increase due to this shortening of generation interval. The correlation between EBV of family members will increase because performance information on sibs and the female candidates is no longer available which

will increase (keeping other parameters constant) the rate of inbreeding. When restricting the rate of inbreeding, the increase in genetic gain is expected to be minimal if not negative. The generation interval should not be regarded as a design parameter for the breeding schemes but needs to be a result of selection across the available age classes while constraining inbreeding.

7.5. Comparing alternative schemes

Maximising genetic gain while constraining the rate of inbreeding will change the layout of breeding schemes compared to simply maximising genetic gain. Following the pioneering work of Nicholas and Smith [26] and subsequently many others, breeding schemes for dairy cattle have moved towards selection based on sib information which enables higher short-term genetic gain. However, for species, such as dairy cattle where the trait of interest cannot be measured on the male selection candidate, maximising genetic gain while restricting inbreeding is likely to move optimum selection schemes back to progeny testing, in particular when population size is small and the constraint on ΔF is stringent [29]. This situation changes when traits of interest can be measured early in life on both sexes, as is the case in beef cattle and pigs. The situation would also change when molecular information was available to predict the Mendelian sampling component of selection candidates at an early age (e.g. [30]). The combination of increased female reproductive rate and DNA markers offers good opportunities to increase gain while restricting inbreeding.

Application of IVEP opens the way for a factorial mating design in which both females and males are mated to several members of the opposite sex. A factorial mating design results in a higher genetic gain at the same level of inbreeding (e.g. [31–33]). Large-scale use of IVEP results in breeding schemes where it is optimal to select fewer dams than sires.

7.6. Embryo cloning

By the creation of large numbers of identical individuals, embryo cloning has the potential to greatly increase accuracy of selection, because each female selection candidate can be evaluated on the average phenotypic performance of many copies of itself. However, when comparing schemes at a fixed testing capacity, testing of clones can only be achieved at the expense of a reduction in the testing of full- or half-sibs. De Boer et al. [34] and Villanueva and Simm [35] concluded that because of this trade-off, cloning would have only a marginal effect on the rate of genetic gain. These studies were performed in dairy cattle where the improved testing was restricted to females only. Cloning offers the opportunity to test selection candidates under different environments, to subject them to a disease challenge that cannot be applied to selection candidates or to measure carcass and meat quality traits directly on selection candidates. Testing clones instead of half- or full-sibs provides more information in these cases because the clones share the Mendelian sampling term with the selection candidate. This advantage would also hold for traits that are subject to genotype by environment interaction. Embryo cloning offers the opportunity to test a single genotype under various conditions.

7.7. Dissemination

Reproductive technologies play an important role in the dissemination of the genetic progress generated in the nucleus population(s) to the commercial population. Embryo cloning could have a large impact in dairy cattle: instead of inseminating commercial cows with semen from high-merit males, embryos of the best available clone in the nucleus population could be used. Having been selected as the best of the clones being produced in the nucleus, the genetic merit will be greater than the average merit of the nucleus population [35,36]. It is important to realise that it is a once-only genetic lift of the commercial population and that the original genetic lag will be restored as soon as cloning of nucleus animals is stopped. This is the same for all measures to reduce genetic lag between the nucleus and commercial populations and makes it more interesting to invest in genetic gain in the nucleus population, as these genetic changes are permanent and can be accumulated over years.

Clones enable widespread exploitation of non-additive genetic effects both within and between breeds. Using cloning in commercial farms to produce replacement animals reduces the proportion of animals that are required to produce replacement cows—the remainder could be used for the production of animals for beef production [21]. This advantage could also be captured by the use of sexed semen or embryos.

In dairy cattle, a gene-based sex determination system ensures that approximately 50% of the offspring will be of the male sex and 50% will be of the female sex. In a dairy cattle production system, this ratio is not ideal. For the dissemination of genetic material, i.e. the production of replacement heifers at commercial farms, only female offspring are desired. Sexing of semen can be applied to achieve this goal. Recent advances in the understanding of the expression and the direct modification of animal genomes, allows us to consider sexual phenotype as a potential target for genetic modification [37].

Visscher et al. [38] described that cloning could lead to the removal of one or two tiers in the pig breeding pyramid. This underlines that new reproductive technologies might have an effect on the genetic gain as well as the structure of the breeding population. Additional factors that play a role in the structure of the breeding scheme are ownership of breeding stock, infrastructure to apply reproductive techniques, control of veterinary status and costs associated with new techniques. The use of crossbred clones in dairy cattle offers a unique opportunity to protect the breeding stock of individual companies. At present, genetic material is freely accessible on the market and this is a stimulus to focus on short-term goals.

8. Economic considerations

Economic aspects of the application of reproductive technologies will be considered for the breeding organisation and commercial farmers. For evaluating economic consequences of alternative strategies for breeding organisations, three approaches can be distinguished. In the first, the financial value of genetic change is evaluated, the second looks at effects on market share and the third looks at the reduction in costs to achieve the desired rate of genetic gain. These three approaches will be described and discussed. In the final section,

economic consideration of using reproductive techniques on commercial farms will be described.

8.1. Financial value of genetic change

In this approach the financial value of genetic change as expressed by improved dairy cows in the population over time is determined. Such evaluations can be carried out following the gene flow approach of Hill [39] and Elsen [40]. Their approach amounts to the computation of the number of genotypes improved by selection over time and by discounting for time of expression. In principle, a breeding scheme with the largest difference between cumulative discounted returns and costs (e.g. for application of reproductive technologies) is optimal. Brascamp [41] showed that the discounted expression can be approximated. Using that approach, financial returns can be evaluated from the annual genetic improvement (ΔG) expressed in monetary units and the approximated discounted expression per cow in the population. Brascamp et al. [42] showed that for a discount rate of 5%, approximated discounted expression per cow lies between 7 and 10 for progeny-testing and MOET breeding schemes.

Let us consider a situation where genetic improvement increased from 1 to 1.1 genetic standard deviation due to improvement in reproductive technologies. For Europe, a genetic standard deviation in the breeding goal for dairy cattle corresponds to € 50 per cow per year. This value depends on the traits included in the breeding goal, the production system and the price of inputs and outputs. The increased genetic improvement of 0.1 genetic standard deviation corresponds with a monetary value of € 5. Using the approximated discounted expressions, the increase in genetic response corresponds with a cumulative financial return of € 35 per cow for a progeny-testing scheme in the population. This value can be interpreted as the economic revenue of expression of genetic merit which on average starts in year 9 (earlier for dam paths and sire to daughter but later for sire to son paths) and ends in year 25. For a cow population of 1 million, the cumulative financial returns are € 35 million. These are the additional returns in the population that result from a single round (1 year) of improved selection by the breeding organisation. The increased costs for the breeding organisation have to be covered by additional returns from sales of breeding stock or semen. However, genetic improvement will probably benefit neither the breeding organisation nor the dairy farmer but will benefit the consumer [43]. The discounted gene flow approach may be seen as a national approach, by which genetic improvement (e.g. lower cost price of milk) ultimately benefits the consumer. An analysis such as this may support national industries in adoption of new techniques in animal improvement. This national approach is also relevant to the position of the entire dairy industry compared with other industries, such as poultry and plants. The approach is, however, less suited to supporting decision making in commercial AI firms that operate on the international market.

8.2. Impact on market share

Dekkers and Shook [44] developed an approach to look at the returns from sale of semen by breeding organisations operating in a large dairy cattle population and with a

Table 2
Effect of pre-selection in young bulls on the proportion of bulls selected after progeny test (basis 10%) for the innovative organisation adopting a new technology, the proportion of proven bulls from the innovative AI firm (basis 25%) and on additional semen sales (×€ 1000) at a discount rate of 0 and 5% for two reactions of competitors (A and B)[a] (adopted from Brascamp et al. [42]).

Alternative	Effect of improved technology (σ_A)	Fraction of young bulls selected	Share in proven bulls used	Cumulative extra semen sales[b] (×€ 1000)	
				$r = 0$	$r = 0.05$
Base	0	0.1000	0.2500	0	0
A	0.15	0.1229	0.3073	4298	2097
A	0.30	0.1476	0.3690	8925	4354
A	0.45	0.1737	0.4343	23,822	6743
B	0.15	0.1229	0.3073	215	160

[a] In alternative A, the innovative firm adopts the improved technology for a period of 20 years and the competitors do not react. In alternative B, the competitors do adopt the improved technology from year 2 onwards (delay of 1 year).

[b] The extra semen sales have been computed for a total of 1 million first AI inseminations of which proven bulls cover 75%. The returns from one successful AI to the firm are € 5.

competitive semen market. Changes in returns for the breeding organisation that adopted an alternative breeding program resulted from changes in market share of semen sales. Improvement of an organisation's breeding programme over that of its competitors increased the organisation's contribution to the pool of active bulls, mainly from increasing the fraction of young bulls selected as active bulls. Adoption of new technology by all competitors in the same way results in no financial return at all. This assumes that all organisations have the same infrastructure in place to capitalise on new technologies. The advantage of implementation by an organisation would create a competitive advantage for a given period of time.

An illustration of this approach is given in Table 2 which is adopted from Brascamp et al. [42]. They determined the consequences of different pre-selection schemes on the competitive position of an AI firm. They looked at the consequences of an increase in EBV of young bulls prior to entering progeny testing and also at the situation where marker-assisted selection lifted the average EBV of young bulls. We have shown that reproductive technologies can affect intensity and accuracy of selection which might also lift the average EBV of young bulls prior to progeny testing. Brascamp et al. [42] showed that an effect of pre-selection of $0.15\sigma_A$ corresponds with an increase in annual genetic gain (ΔG) of $0.03\sigma_A$.

When pre-selection increased the mean breeding values of bulls entering progeny testing by $0.15\sigma_A$, the fraction of young bulls selected after progeny testing to be used as proven bulls increased from 10 to 12.29% (Table 2). The share in the pool of proven bulls in that case changed to $1.229 \times 0.25 = 0.3073$, where 0.25 reflects the size of the AI organisation. The market share increased to 43.4% when the effect of improved pre-selection was $0.45\sigma_A$.

To calculate the additional returns from semen sales, a population of 1 million cows is assumed of which 75% are inseminated with semen from proven bulls with a semen

price of € 5. In that case, 1% market share corresponds to an annual return from semen sales of € 37,500. When the effect of pre-selection is $0.15\sigma_A$, the change in annual returns from semen sales equalled $(30.73 - 25) \times 37,500 =$ € 214,875. For alternative A, the total financial returns from semen sales (obtained in years 6–25) as a result of improved pre-selection was € 4.3 million. For the alternative in which competitors adopted the new technology 2 years after the first firm adopted it, the additional undiscounted returns were € 214,875, which resulted from an increased market share in year 6 only (Table 2).

The results show very clearly that the effects of implementing a new technology depend largely on timing. The returns are larger when competitors are slow in adopting the new technology. Furthermore, the total size of the potential market for semen sales and the number of bull progeny tested play an important role. In the international market, the situation in which one firm adopts an improved breeding scheme might be seen as a country changing its breeding programme. In that case, the additional revenues will come from export of semen.

8.3. Application of reproductive techniques by commercial farmers

Reproductive technology is also used in the dissemination of genetic material from the nucleus (breeding organisation) to the commercial farmers. De Boer and Van Arendonk [36], for example, concluded that the main advantage of cloning is faster dissemination of superior genetics to commercial farmers using cloned embryos from desirable genotypes. A dairy farmer's decision to inseminate a cow with a progeny tested sire or to implant a cloned embryo from a tested female genotype into a cow depends on factors determined by the breeding scheme, such as the difference in genetic merit between available semen and cloned embryos [35]. Other factors, such as the difference in purchase price between cloned embryos and semen, also affect the decision. The market share for cloning increases when the superiority of cloned embryos over semen increased. Use of sexed semen would ensure that all calves born from AI were females. As a result, fewer cows would be selected for AI to produce replacement heifer calves. Use of sexed semen would lead to higher average genetic merit of newborn heifer calves than when unsexed semen is used. The use of cloned embryos or sexed semen would also reduce the number of cows that are needed for the production of replacement heifers. This offers the opportunity to increase the fraction of cows that are used for the production of (crossbred) beef animals or to prolong the lactation length of cows. The use of sexed semen or embryos also offers an opportunity for the farmer to reduce calving difficulties and thereby improve animal welfare.

9. Other considerations

In this manuscript, we have concentrated on the impact in genetic terms of reproductive technologies. For breeding companies and farmers, the costs of applying reproductive technologies are an important issue. In this manuscript, we have seen several examples of how reproductive technologies can be used to increase genetic gain

for a given rate of inbreeding. Application of the new technology is likely to increase the costs of the breeding programme. One can, however, also evaluate the costs of alternative breeding schemes to achieve a given level of a genetic improvement. Under that scenario, new technologies are not used to increase the genetic response but to reduce the costs of a breeding scheme while maintaining the same level of genetic improvement or the same market share.

An important economic consideration for breeding companies is the protection of ownership of unique genetic material. This aspect is not captured by any of the approaches described for economic evaluation. As mentioned earlier, the application of cloning could lead to a change in the breeding structure that enables a better protection of ownership. The economic benefits of this for the breeding organisation are potentially large.

The application of reproductive technologies in animal breeding raises ethical questions, principally related to animal welfare. Even if these animal welfare issues are successfully addressed, the debate about the ethical acceptability of technologically highly advanced animal breeding will continue. Scientists involved in the development of technologies and those considering their application are and should be involved in this debate (e.g. [45,46]).

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