

STRATEGIES TO IMPROVE BALI CATTLE IN EASTERN INDONESIA

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Options for Genetic Improvement of Bali Cattle — Assessing the Strengths and Weaknesses of Alternative Strategies

Option 1. Full program with all technologies and facilities available

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Abstract

There are many reproductive technologies available to cattle breeders and those breeders or, more particularly, groups of breeders who use them will need to shift their breeding and selection practices and philosophies to get maximum benefit from them. Techniques such as artificial insemination, multiple ovulation and embryo transfer and cloning have the capacity to increase fecundity many-fold in individual animals. Others, such as molecular assisted selection, may assist in improving accuracy of selection for individual traits. Boosting reproductive performance can enhance genetic gain considerably, but at both a financial and genetic cost. The major genetic penalties are the increase in inbreeding and loss of genetic diversity. By using a program called GENUF we can predict the sort of improvement in genetic gain that is possible. This paper discusses the magnitude and importance of a range of technologies in improving genetic gain. In general, reproductive technologies have much greater impact than molecular assisted selection, which should be confined to areas where it has maximum benefit such as carcass traits and disease resistance.

Introduction

In any animal breeding operation there are two key questions to ask:

- Where to go?
- How to get there?

‘Where to go?’ is about breeding objectives. There are two basic approaches to developing breeding objectives. One is to describe the types of animal we would like to breed. We can do this most efficiently if we use a method or computer program that constrains our thinking to the range of possible genetic change that can be made. The other approach is to be more economically rational, calculating the economic benefits of each unit change in each trait of commercial importance.

‘How to get there?’ relates to the methods that we can use to most efficiently generate genetic change in the desired direction. This involves a range of issues, including the following:

| Issue | Comment |
|-------------------------|--|
| Selection value | As indicated by estimated breeding values |
| Inbreeding | Avoid loss of merit and genetic variance |
| Crossbreeding value | Breed differences and heterosis |
| Connection | Comparing animals from different groups |
| Assortative mating | Elite matings, giving longer-term gains |
| Measurement strategies | e.g. progeny testing; multi-stage selection |
| Quantitative trait loci | Detection and use of ‘major genes’ |
| Parameter estimation | e.g. heritability — good for longer-term gains |

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² Multiple ovulation and embryo transfer

| Issue | Comment |
|---------------------------|---|
| Lifetime value | For ongoing harvesting and reproduction |
| Reproductive manipulation | MOET ² , IVF, sexing, cloning etc. |
| Running costs | Number of breeding females, semen costs, etc. |
| Risk | Staying in business |

Ideally, we need to pay attention to all these issues — and we need to tie them strongly together, using progressive information systems. This paper discusses what can be done if there are no constraints on funds, resources and expertise.

Reproductive Technology and Designs to Exploit it

Reproductive technologies such as artificial insemination (AI) and multiple ovulation and embryo transfer (MOET) can be used to increase fecundity by a large amount. This increases selection intensity and, in turn, genetic gains.

The best design for a breeding program often changes when these technologies are used. As someone once said, turning a cow into a sow means we should shift from cattle to pig designs.

Cloning is an extreme form of reproductive boosting. It has different consequences for breeding and production programs because it does not involve production of genetic variation through sexual propagation.

Multiple ovulation and embryo transfer

In MOET, females are superovulated by hormone injection and mated; multiple embryos are then collected and transferred to host females. These host females play no part in the genetics of the breeding program.

Unfertilised ova can be collected from both adult and juvenile females in a process referred to as oocyte pickup. A description of the state of the art in MOET, oocyte pickup and related technologies is provided in Kinghorn (2000b).

MOET improves the rate of genetic improvement because of the favourable effects of high reproductive rate on three key factors:

- increased selection differential;
- reduced generation interval;
- increased accuracy of estimated breeding values.

Increased selection differential and reduced generation interval

The above factors can be shown by example, using the program GENUP, which can be downloaded from Website <http://metz.une.edu.au/~bkinghor>.

If you want to try this example, run the GENUP module AGES, and:

If the default GENUP data set has been retained, you should find a response of 0.077 kg fleece weight per year. Optimise age structure and this should increase to 0.082 kg per year, keeping males and females for 2 and 4 matings respectively. For help in running AGES, hit key F1 after loading it.

Without MOET the weaning rate is taken as 0.95 lambs weaned per ewe mated. Increase this fourfold, to 3.8 lambs weaned per donor ewe mated, to simulate MOET, and optimise age structure. The response should increase from 0.082 kg to 0.1412 kg. Notice that this affects the values of selection intensity, i , and generation interval, L , considerably, and the optimum age structure is now considerably younger — keeping males and females for 1 and 2 matings respectively.

Notice that with MOET we have both higher selection intensity and lower generation interval for both sexes, not just females: higher reproduction means fewer females to get the same number of progeny — and these fewer females can be mated by fewer males!

Notice also that with MOET, the figure of 1000 breeding females relates only to superovulated donor ewes. The breeder needs to maintain a large pool of recipients, making this a very expensive program to run.

Increased accuracy of estimating breeding values (EBVs)

Recall that increased accuracy of estimating breeding values leads to wider distributions for EBV. This is illustrated in Figure 1.

Figure 2 illustrates the value in placing more emphasis on measuring males. The lower proportion required for breeding can be capitalised on by more measurement and thus wider EBV distribution.

We can use this approach to illustrate the effect of boosting male and female fecundity through AI and MOET (Fig. 3).

Natural matings EBVs calculated properly from a selection index calculation or a BLUP analysis have one very useful property: The predicted merit of progeny is simply the average of the EBVs of the two parents used, as shown in Figures 2 and 3.

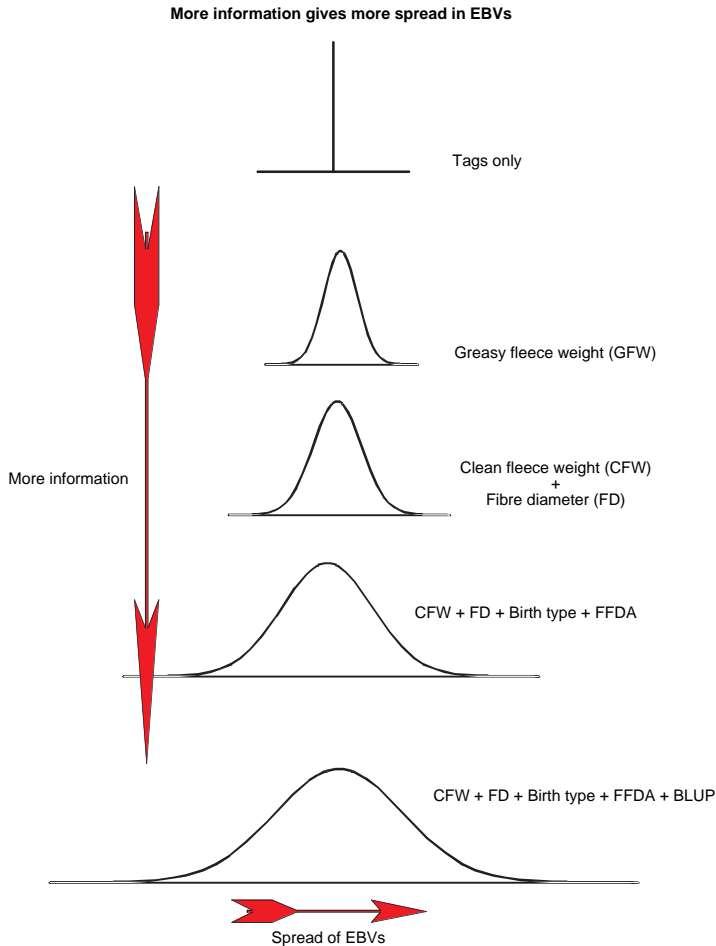


Figure 1. The relationship between amount of measurement made and the width of EBV distributions.

If the only information available is animals' tag numbers, there is no power to identify superior (or inferior) animals and no variation in EBVs.

If GFW is known there is some such power — and yet if FD is of key importance in the objective this power is obviously limited. Animals of exceptional breeding value are difficult to identify as the most important trait is not measured.

As more information is gathered, there is more power to identify animals of low and high breeding value, and the EBV distribution widens.

Information from relatives also helps here, as in the distribution at the bottom, which uses BLUP genetic evaluation.

A smaller proportion of rams than ewes can be selected for breeding, contributing to their high mean EBV. The other factor, in this case, is the greater amount of information used to calculate ram EBVs, reflected by a wider EBV distribution. If using MOET, the value of taking more measurements in ewes (as well as rams) becomes higher.

Notice in Figures 2 and 3 that the predicted merit of progeny is simply the average (or half-way point) between the selected rams' and ewes' mean EBVs.

The width of the EBV distribution of the progeny depends on how intensively they are measured.

AI: increased selection intensity With the use of AI the best few rams can be selected for breeding. This means that the average EBV of rams used is higher, as can be seen in Figure 3 — only the very best rams contribute to the average EBV of rams. This increase is diluted 50% by the ewe contribution, but in Figure 3 the net increase in predicted merit of

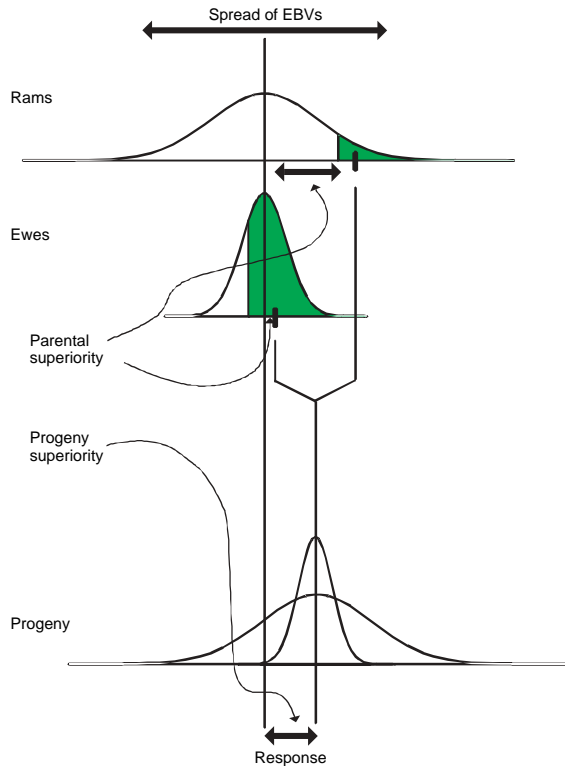


Figure 2. Response to selection over one generation depends on accuracy of selection (reflected in width of EBV distribution depicted by the bell-shaped curves), and proportion selected. Males are measured more here, giving wider distributions.

progeny is quite visible compared with natural mating, where the selection intensity of rams is lower.

MOET: increased selection intensity and more information for estimating breeding value With MOET, each selected ewe can contribute not just one or two lambs, but up to about six lambs per donor ewe, a figure which continues to improve. As with AI, this brings about the ability to select fewer ewes as donors of genetic material (though many recipient ewes are still required to carry the lambs). Moreover, in an ongoing breeding program using MOET, candidates for selection will usually have a number of full brothers and sisters available with records. This information helps to improve the accuracy of EBVs, and the distribution of EBVs increases accordingly. Both these favourable effects are seen in the bottom diagram in Figure 3.

The favourable effects of reduced generation interval cannot be shown in this simple manner, but are discussed in the next section.

Even so, Figure 3 shows that AI and MOET, if properly used, can bring about a notable increase in

the response to selection. Current theoretical predictions suggest that a MOET program will give up to about 25% extra gain over a normal breeding program. Steps to avoid increased rates of inbreeding have moderated predictions substantially.

Juvenile MOET schemes versus adult MOET schemes

Beef MOET schemes differ from dairy MOET schemes because key traits can usually be recorded before or close to sexual maturity, rather than well after this stage as in dairy cattle. Figures 4.1a–c illustrate the life history in an adult MOET scheme for beef cattle.

A ‘juvenile’ MOET scheme in beef implies collecting oocytes before sexual maturity, as in Figure 4(a).

In Figure 4(b) the oocyte pickup is carried out on 6 month old females (e.g. 21 months into the scheme) based on their parents’ records (at 14 months). In Figure 4(c) the oocyte pickup is carried out on 3 month old females (e.g. 15 months into the scheme) based on their parents’ records (at 14 months).

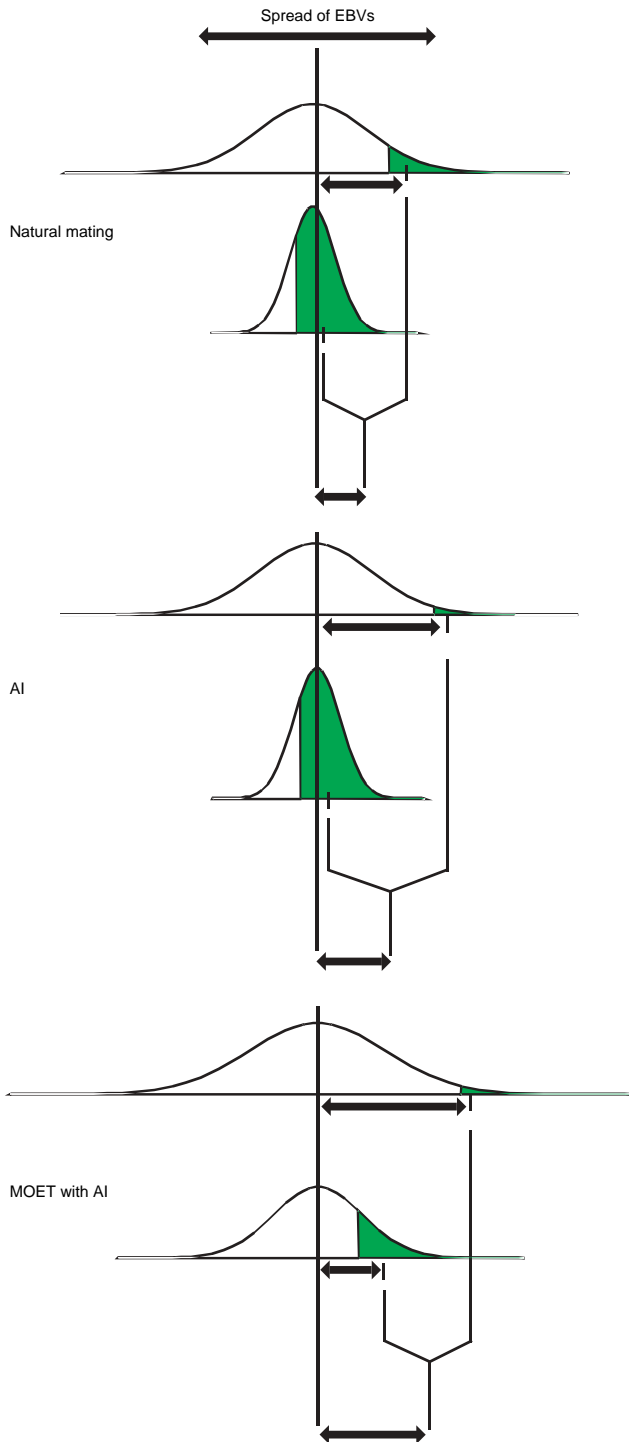


Figure 3. The impact of AI and MOET (middle and lower diagrams) on selection response, compared with natural mating (upper diagram). Refer to Figure 2 for orientation and to text for explanation.

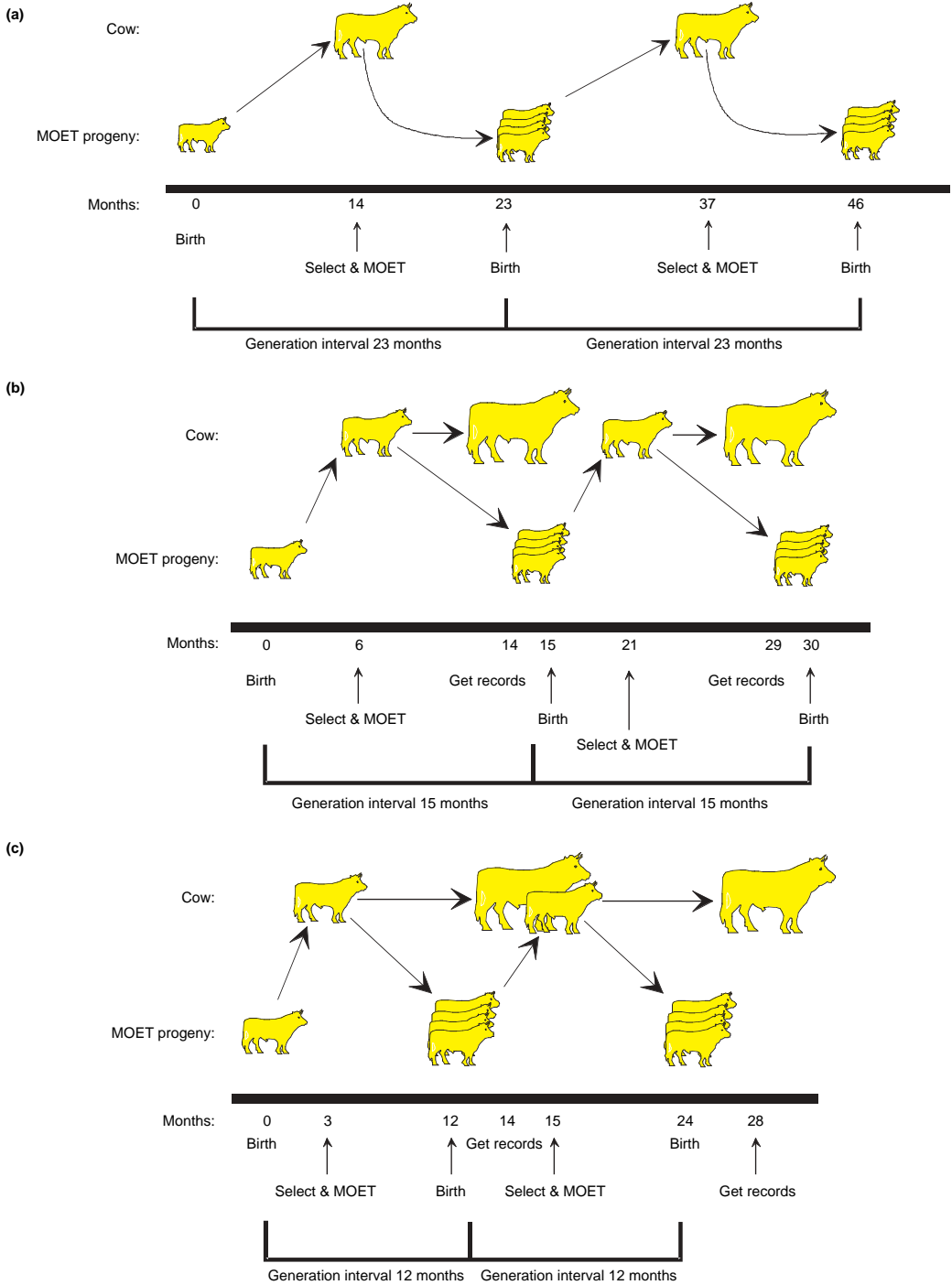


Figure 4(a-c).

Carrying out oocyte pickup earlier than 3 months (see JIVET below) means that slaughter records on 14 month old parents will not be available. Again, information from genetic markers might well make oocyte pickup of value at younger ages, even pre-natally.

Juvenile in-vitro embryo transfer (JIVET) JIVET involves collection of ova from sexually immature females, followed by in-vitro fertilisation (IVF). JIVET has already been implied in the last selection, wherever fertilisation takes place in vitro.

Techniques for manipulating waves of follicular activity have resulted in recovery of high numbers of oocytes from females. This has also been successful at a research level with juvenile animals such as six week old lambs and eight month old calves, whereby the reduction in generation interval is expected to lead to notable increases in rates of genetic gain. However, it should be noted that there are considerable animal welfare issues associated with these procedures on juvenile animals.

By carrying out IVF it is possible to mate each female with many males. If we can collect an unlimited number of eggs, a good design is to mate every male and female together in a cross-classified design. Simulation results suggest that such a scheme could give twice the response to selection that a full national dairy program can, with similar rates of inbreeding (Kinghorn et al. 1991).

If we succeed in having a high degree of control over fecundity, we are left with the decision of how best to use it. Reproductive boosting gives higher genetic gain, but at a penalty of increased inbreeding and lost genetic diversity. At the extreme it also constitutes high risk, by 'putting all the eggs in one basket'. These problems can be handled in an appropriate mate selection scheme, such as Total Genetic Resource Management (TGRM) (Kinghorn 2000a).

Sexing of Semen or Embryos

Sexing of semen or embryos has long been a dream of animal scientists. There has been a long history of effort in this area, but there are prospects for practical implementation in the near future. As with cloning, the main impact of semen sexing is to raise efficiency of production systems rather than to improve the rates of ongoing genetic improvement.

The value of sexing for genetic improvement programs

Sire selection is the main driver of most breeding programs — because we need to select only a small number of sires from the same number of candidates as we have for dams. However, it is interesting to contemplate that if we generated fewer male candidates and more female candidates, perhaps making

the selection proportions equal, we might make better selection responses. Unfortunately, as Figure 5 shows, this approach leads to very little extra selection response. Using such simple models, it is difficult to generate a prediction of more than 5% extra response compared with using a 50:50 sex ratio.

However, we can improve on this for production systems such as dairy, where key measurements can be made only on females. The argument is not simple — we would still need to milk more females to get more information, and milking spaces are usually the limiting factor. Increasing the number of female offspring from matings to progeny test young bulls would lead to higher selection accuracies, and/or the ability to test more bulls. Increasing the number of male offspring from elite matings contracted by breeding centres to produce bull candidates for progeny testing would also give some benefits, essentially increasing pressure on the cow-to-breed-bull pathway.

Semen or embryo sexing can be used as part of an IVF program to help improve response. However, results have been disappointing. Sexing in the cross-classified dairy scheme described earlier added only between 1.3% and 3.0% to predicted response. This sort of gain is unlikely to be worth the cost and the reduction in birth rate, which were not accounted for in the study by Kinghorn (2000b).

Sexing of semen and embryos holds much more promise for animal production systems than for genetic improvement systems (Kinghorn 2000b).

Cloning Technology and Designs to Exploit It

Introduction

Cloning is an extreme form of reproductive boosting. Clonal propagation has long been used in plant breeding. It exploits the genes in the best individuals, but it also exploits the favourable way in which these genes work with each other in these individuals. Such favourable partnerships can be broken down when they are mixed with other genes in the normal breeding cycle.

Thus, clones are somewhat static — they are good at providing high productivity, but not so good at creating future generations of better-performing individuals. The latter requires genetic variation — variation from which the new elite can be chosen.

This variation is generally not lost with other forms of reproductive boosting such as oocyte pickup (Kinghorn 2000b). These can lead to some of the direct benefits of clones, through widespread use of elite individuals, but with a maintenance of genetic diversity which can lead to further gains in the following generations.

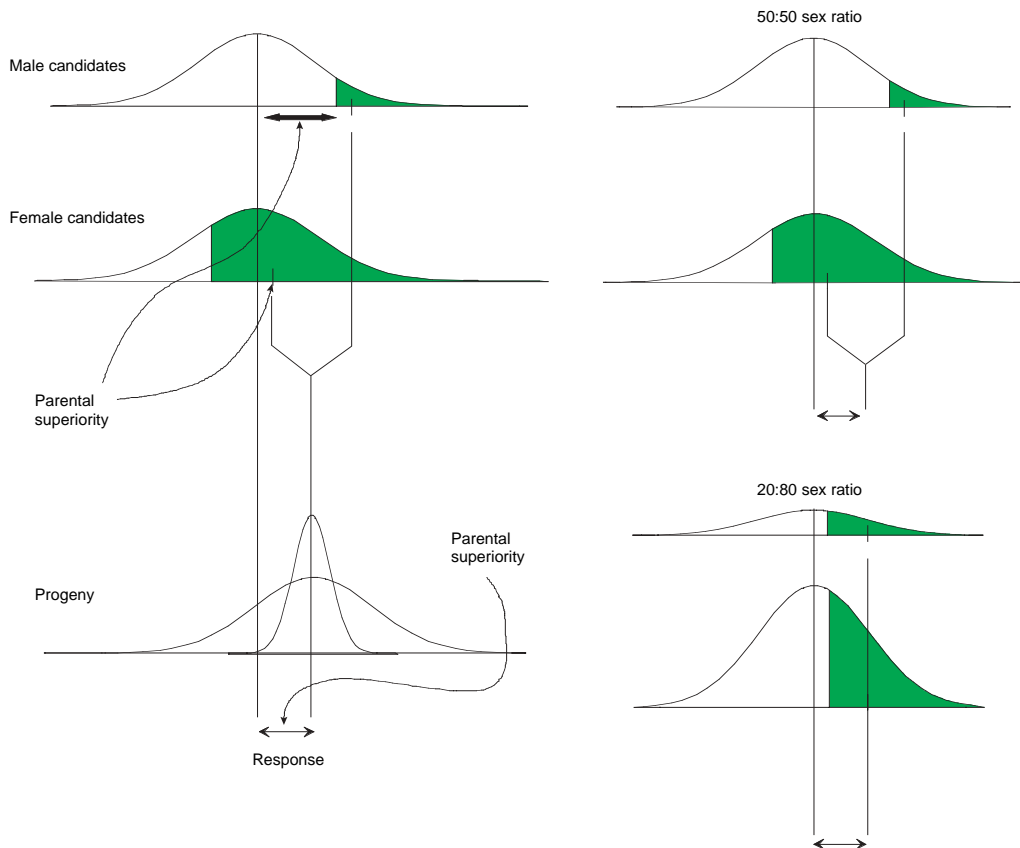


Figure 5. The left half of the figure illustrates selection in males and females on EBV, and transmission of the resulting superiority to the progeny generation. This is repeated more simply at upper right, with a 50:50 sex ratio. At lower right, the sex ratio has been altered using semen sexing such that there are more female candidates than male candidates for selection — and yet the same number of candidates of each sex need to be selected as parents (the shaded areas have the same area as for 50:50 sex ratio). Notice that semen sexing has added little to response.

We can now generate genetically identical individuals from embryonic or even adult tissue (Kinghorn 2000c). For current processes using nuclear transfer, the nuclear genes are identical between clones. Only the cell organelles are non-identical. We cannot know that the resulting animals will be genetically elite — we can only aim at this by using elite parents to generate embryonic tissue, or using elite adults that have performed well. This section considers how we might choose which animals to clone, how to use the clones, and what impact this might have.

A simple example

As with normal breeding practices, luck can still play a big role in the choice of individuals to clone. Figure 6 compares exploiting a superior ram, either

through cloning or through generating progeny. First of all, some of the ram's observed superiority of 1 kg fleece weight is expected to be due to luck in the environmental factors which have affected his performance. This accounts for about 40% of his performance at the top of the left-hand bar in the diagram.

About 40% (the heritability of fleece weight) of his performance is expected to be reflected by the value of his genes to his progeny, giving an EBV based on his own performance of 0.4 kg. However, favourable interactions among his own genes are expected to result in about 60% of his superiority being due to the value of his own genes to himself. This is also the expected value of his genes to his identical clones, such that the expected superiority (merit) of his clones is not 1 kg, but 0.6 kg.



Figure 6. Merit of clones and merit of progeny from a ram with a 1 kg superiority in fleece weight.

If the ram is mated to average ewes, the performance of his progeny is expected to be the average of his EBV (0.4 kg) and that of average ewes (0 kg superiority), or 0.2 kg. Thus cloning would be expected to yield about three times as much extra merit (0.6 kg) versus 0.2 kg. Whether we could spread an individual's genes as widely through cloning as we can through AI remains to be seen.

However, these predictions of clones and progeny merit are exactly that — predictions. The actual outcome in any one case is subject to luck. The ram may not have had a particularly favourable environment, and his clones could well be as good as he is. However, on average across all such cases, the clones will not perform as well.

We can minimise the risks involved by using good data records, and using them properly with due attention to how we want to use the clones.

Genetic evaluation using clones

One key use of clones is to make genetic evaluations. There are two parameters that we may want to estimate:

- *Breeding value.* This is the value of an animal's genes to its progeny. We want to make estimates of breeding values (EBVs) whenever we want to make judgments about breeding animals for generating progeny. We also need EBVs when making decisions about which animals to clone, if the clones are to be used for breeding rather than production — as in the cloning of bulls to use widely for natural mating.
- *Genetic value,* or genotypic value. This is the value of an animal's genes to itself. We want to make estimates of genetic values (EGVs) whenever we want to select animals to make clones of themselves to generate product to be harvested.

We can estimate both breeding and genetic values from a number of sources. However, two key sources to be examined here are progeny and clones. Kinghorn (2000c) gives the predicted accuracy for

selection on breeding value and on genetic value, when progeny or clones are the source of data.

Figure 7 uses the prediction equations to show these accuracies of evaluation. For this result, narrow-sense heritability was taken as $V_A^*/V_P^* = 0.25$ and broad-sense heritability as $V_G^*/V_P^* = 0.45$. This assumes that the way that genes interact within individuals has quite a major influence on their performance, explaining 20% of observed variation (0.45 minus 0.25). This value is well within the range reported.

For a small number of progeny or clones tested, clones give more accurate evaluation, because they share all of their genes with the animal being evaluated, as opposed to only half in the case of progeny. However, clone data contain some unwanted baggage for the estimation of breeding values. This is the component of genetic value that is due to the particular interactions between genes in each individual: for example, an animal that has a favourable heterozygous state at a given gene locus (i.e. dominance expressed due to inheriting different gene variants from its two parents) cannot transmit this benefit to its offspring — it can transmit only one variant and not both. The mean of many clones contains this benefit, which is unwanted bias when estimating the breeding value of this animal.

Thus using clones to evaluate breeding value is not competitive with normal progeny testing for more than about 16 progeny or clones recorded (Fig. 7). When very many progeny are tested almost full breeding value accuracy is reached — after all, breeding value is about the value of an animal's genes to its progeny. However, when very many clones are tested the highest breeding value accuracy is limited, because of the unwanted influence of the components in genetic value that cannot be transmitted to the next generation.

* V_A = additive variance
 V_G = genetic variance
 V_P = phenotypic variance

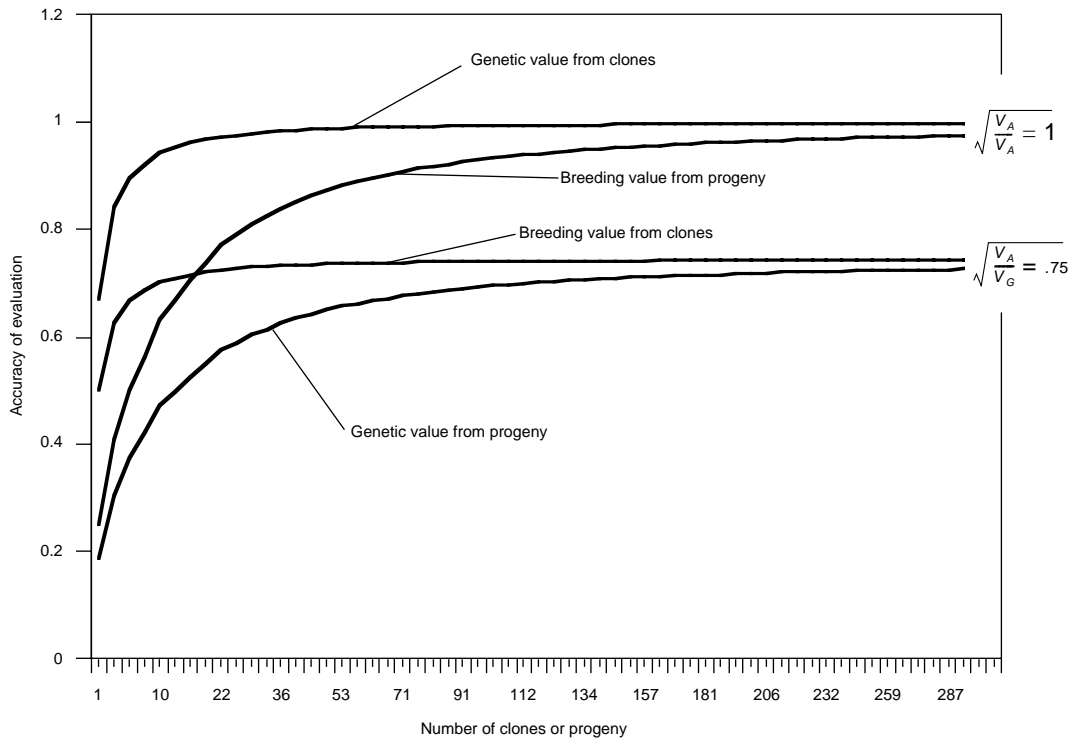


Figure 7. Accuracy of evaluation of breeding value and of genetic value when the source of information is records on n progeny or n clones. See text for assumptions.

Genetic gain from cloning

This limit in the value of clones for estimating breeding value, together with the much higher cost of cloning, helps to illustrate why clones are not expected to be of great value in generating faster ongoing rates of genetic change. The other factor against clones in this regard is the narrowing of the genetic pool: there are far fewer genetically distinct individuals within breeding programs using clones, leading to higher inbreeding and lower genetic variation in the longer term.

Using a simulated dairy population, de Boer et al. (1994) predicted a 1.4% increase in the ongoing rate of response through clone testing for milk production traits, while maintaining similar inbreeding levels, in the absence of genetic dominance. There was no increase in the presence of dominance. However, they did find useful improvements in production levels due to clones, and concluded that reliable commercial clone lines could be produced effectively, presumably if costs are sufficiently low.

One major disadvantage of using clones in dairy breeding programs is that we cannot carry out a clone test on a bull for milk production. However,

clone tests can be useful in any species for traits that require sacrifice for measurement, such as many carcass traits and some disease resistance traits. This is the most promising area for using clones to increase ongoing rates of genetic gain.

Production gain from cloning is expected to be much more fruitful (Kinghorn 2000c).

Molecular Genetics

Molecular genetics and their place in breeding systems have already been described during this workshop (Van der Werf and Kinghorn 2002). This paper will make a simple illustration of the value of marker-assisted selection using simulation. It should be noted that markers for easy-to-measure traits such as growth are expected to be much less valuable than markers for traits such as disease resistance and carcass traits.

Information systems

Figure 8 illustrates the relationships among some of the key progressive information systems in animal breeding.

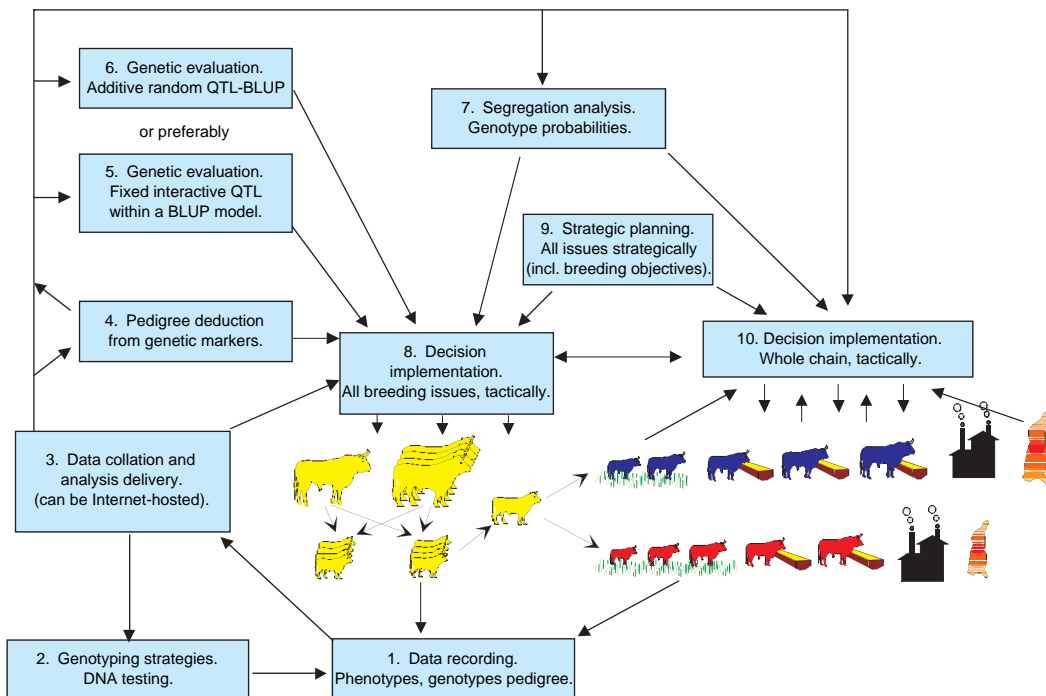


Figure 8. Some key information systems in animal breeding.

The rest of this section briefly describes the different information systems shown in Figure 8.

1. *Data recording*: This is a key component. In some cases special tools and methods are required to make measurements, especially for traits related to carcass quality and disease resistance.
2. *Genotyping strategies*: Genotyping is becoming increasingly widely practised, with applications using both genetic marker loci and known gene loci. The cost of genotyping is generally high, such that inferring genotype from the known genotypes of relatives and/or linked loci has the potential to play a useful role in reducing costs. Segregation analysis, described below, can be used for calculating genotype probabilities. These in turn can be used in an iterative genotyping strategy — they are used to help choose which individuals and loci to genotype in each iteration (see for example http://www.beef.crc.org.au/publications/bkinghor/aaabg99_359.pdf). Individuals and loci to be genotyped in each cycle are chosen in a manner designed to maximise the utility of the resulting information across the whole population. Genotyping can proceed until perfect information is known on all individuals of interest (which can be accomplished with only

part of the population actually genotyped), or it can proceed until a nominated genotyping cost has been spent, or until some function of utility and cost has been maximised.

3. *Data collation and delivery of analysed data*: Our experience is that the Internet facilitates very effective distributed deployment of services using operators located close to end-users/customers. Data and software are fully up-to-date — we now have fully automatic upgrading of client software, with no action by operators other than launching the application. Internet hosting also provides software security, full tracking of activities for billing purposes, excellent opportunities for technical support, a simpler path to scaling up operations, and opportunity for e-commerce of products as well as services.
4. *Pedigree deduction*: Good method and software can be used to solve complex parent-allocation problems — such to deduce the parents of 250 progeny out of a syndicate mating of 300 cows and 10 bulls. An appropriate feature is to go beyond allocation by exclusion, to using marker genotype probabilities. This will enable a reduction in the number of marker loci run — one target being to have just one multiplexed marker

set. For example software, see Tristan Marshall's 'Cervus' at <http://helios.bto.ed.ac.uk/evolgen/cervus/cervus.html>.

5. *Genetic evaluation — fixed interactive quantitative trait loci (QTL) within a Best Linear Unbiased Prediction (BLUP) model*: This is a preferred approach to genetic evaluation (see for example <http://www.beef.crc.org.au/publications/bkinghor/allerton.pdf> or, more concisely, <http://www.beef.crc.org.au/publications/bkinghor/isag98.pdf>). Direct or 'diagnostic' markers are simplest to use here, as we can treat them as fixed but interacting effects. Operationally, they almost remove the need for trait measurements and pedigree information. (However, multiple allelism means that only complete sequence markers are fully reliable, as otherwise alleles of identical marker type can have different effects.) For linked markers, we can modify transmission probabilities in segregation analysis to calculate QTL genotype probabilities. Typically two QTL alleles would be considered to be involved and QTL genotype effects treated as fixed. This is probably preferable where few effectively distinct alleles are known to be segregating, and where dominance and/or epistasis are important.
6. *Genetic evaluation — additive random QTL within a BLUP model*: This is increasingly being used for genetic evaluation where genetic marker information is available. It is a relatively simple extension of classical method. Markers are used to infer the probability of identity by descent of contributing QTL alleles, with QTL effects treated as random and no assumption about the number of alleles at each QTL. However, it aims to evaluate more accurately the average genetic merit of individuals for given traits, and misses the added opportunities to exploit the known mode of action of discovered genes, and the interactions among them that we increasingly find to be important. Without modification or extension, it misses out on the potential marketing advantage of labelling individual animals with probabilities of carrying certain gene variants. It also misses out on ability to target outcomes with respect to the marked genes, which is especially important for non-additive modes of inheritance.
7. *Segregation analysis*: This type of analysis is the key to a number of genetic information systems, including items 2, 4, 5 and 8 in this list. Kerr and Kinghorn (1996) have developed a method that operates on large populations.
8. *Decision implementation for breeding*: A new method makes tactical decisions on selection

and mate allocation in animal breeding systems. This is total (tactical) genetic resource management (TGRM), which integrates technical, logistical and cost issues affecting breeding decisions into a single framework (Kinghorn 2000a).

9. *Strategic planning tools*: This can be thought of as 'strategic genetic resource management', SGRM. The idea is to integrate a range of design evaluation and planning tools into a single project-planning framework. The program 'Z-Plan' from Gerhard Nitter can be used to evaluate a range of animal breeding designs. Various other components have been produced, including cohort-based simulation of optimal strategies for major genes and crossbreeding, predictors of genetic gain and inbreeding under realistic conditions, and variation in outcome to give risk assessments.
10. *Decision implementation for whole supply chain: Total Resource Management*. This is the subject of current research in the Australian Beef Quality Cooperative Research Centre.

Design in animal breeding and production programs is classically implemented through sets of rules to be followed. However, a tactical approach uses all prevailing information to develop an action report that dictates management decisions directly. These problems can be very complex, with no hope of solution using analytical methods. However, evolutionary algorithms have proved to be very powerful in this regard. There has been good success in developing and implementing such a tactical approach in animal breeding, using evolutionary algorithms for optimisation (see 8 above). For other parts of the supply chain, a simple example has been developed so far, involving feedlotting one starting group of cattle to four different end-points of date and target body weight. The objective function included management costs, feed costs and penalties for missing target weights. Parameters optimised are pattern and dates of drafting into sub-groups, and feeding levels over time within each sub-group (see http://www.beef.crc.org.au/publications/bkinghor/AI99_BK.pdf).

Potential Genetic Responses

This section will use computer simulation to give a feel for the potential impact of reproductive and molecular technology on responses to selection. The Genup module PopQTL was used to simulate a population with parameters as shown in Figure 9.

In the following table, AI is represented by using just 2 sires over 200 dams, rather than 8 sires over



Figure 9(a-c).

200 dams. MOET is represented by cows that calve leaving three offspring rather than just one. Molecular assisted selection (MAS) is represented by genotyping of a known gene at an initial frequency of 0.1, the effects of one and two copies of this gene being 3 and 5 units (0.3 and 0.5 of a phenotypic standard deviation) compared with having zero copies.

Table 1. Results after 20 years of breeding, depending on use of technology. Two replicates are shown for each treatment. Note that these results are very highly dependent on conditions assumed, and must be taken as a rough guide only.

| AI | MOET | MAS | Response (%) | Inbreeding (F) | QTL freq. |
|----|------|-----|----------------|------------------|----------------|
| × | × | × | 23.70 20.64 | 0.0676 0.0538 | 0.129 0.670 |
| ✓ | × | × | 28.04 28.31 | 0.2193 0.2067 | 0.386 0.458 |
| ✓ | ✓ | × | 38.80 37.72 | 0.2226 0.3426 | 0.963 0.823 |
| × | × | ✓ | 22.16 21.82 | 0.0589 0.0585 | 0.918 0.977 |
| ✓ | × | ✓ | 27.77 21.05 | 0.1866 0.1735 | 0.985 0.980 |
| ✓ | ✓ | ✓ | 39.82 31.63 | 0.4011 0.3417 | 1.000 1.000 |

In these scenarios, reproductive technology has much more impact than molecular technology. However, it must be remembered that MAS is of less use for traits that are easy to measure, are expressed in both sexes, and are expressed before selection. Moreover, the longer-term consequences of MAS are lower because favourable genes can be selected 'unintentionally' by normal methods over longer periods. These factors underline the fact that any QTL mapping work should be directed at traits for which MAS has higher benefit — such as disease resistance and carcass traits.

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