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# **Developing straight-breeding and cross-breeding structures for extensive grazing systems which utilise exotic animal genetic resources**

*J.P. Gibson & L.V. Cundiff*

*Centre for Genetic Improvement of Livestock,  
Dept. Animal & Poultry Science, Univ. Guelph, CND-N1G 2W1,  
Guelph, Ontario, Canada*

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In this chapter we consider how exotic germplasm can be evaluated and then incorporated into cross-breeding programmes. We define exotic as meaning any breed or strain that is not native to the country or region in consideration. The general principles of how to design and operate cross-breeding systems or create new synthetic populations based on indigenous genetic resources are dealt with in the previous chapter and are not repeated here. Here, we deal with what needs to be modified when exotic germplasm is being considered. We also consider the possibility of using exotic germplasm as pure-breds.

When considering the use of exotic germplasm, the following key questions need to be answered:

1. How can one decide what characteristics should be sought in exotic germplasm?
2. How should one choose between pure-breeding versus creation of a new synthetic versus alternative cross-breeding structures for utilising exotic germplasm?
3. How should choices be made among sources of exotic germplasm for possible importation and testing in the country or region of interest?
4. How should exotic germplasm be imported?
5. How should exotic germplasm be evaluated in local conditions?
6. How should exotic germplasm be incorporated into local cross-breeding systems?

Answers to these questions are not independent of each other and while the above forms a logical sequence for the questions, to obtain a final answer a certain amount of iteration is required. We will deal with each of these questions in turn and then suggest a decision tree for design and implementation of cross-breeding systems based on exotic germplasm.

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## **Introduction**

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## **1. What characteristics are sought in exotic germplasm?**

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In all cases exotic germplasm will be sought to increase one or more aspects of the economic and/or social value of the livestock production system. This will mean increasing the off-take of animal products from the system and/or the number of animals maintained. For either of these goals to be achieved, there must be resources available that the current livestock are not utilising.

These extra resources might be found by improving the efficiency of utilisation of existing resources. It is a general observation, however, that animals with high genetic potential for production generally have higher maintenance requirements and lower ability to thrive on poor nutrients. Thus, in most cases, exotic germplasm is unlikely to find extra resources through improved efficiency. Exotic germplasm might achieve more efficient utilisation of resources if it has higher tolerance of environmental stress, parasites and disease, thereby reducing losses and allowing more resources to flow into production of products or maintenance of larger populations.

If more efficient utilisation of resources is not possible through increased stress tolerance, surplus resources for livestock production must be available if use of exotic germplasm is to be considered. It is therefore important to first document the nature and stability of these resources, before going on to assess what type of genetic changes might be utilised. An integral part of this process is a simultaneous assessment of how the indigenous livestock utilises the resources available and what limits their productivity in that environment.

It is a general observation that high production genotypes also have high maintenance requirements for nutrients and very often, high requirements for management inputs such as shelter and prophylactic protection against parasites and disease. This can make high production genotypes very susceptible to loss of resource inputs. It is a frequent characteristic of low to medium input environments that they are also variable environments. An integral part of the assessment of what type of genotype would improve the current production system is the assessment of impacts of fluctuations in resource supply, brought about by climate fluctuations, long-term trends in physical environments, social and political unrest, changes in local or global commodity prices and war.

While increased productivity is generally desirable, in many situations livestock is extremely important as a form of economic and social capital. There will be situations in which increased productivity in the long-term is obtained at the expense of increased variance in survival. Such increased variance may lead to a proportion of families losing their livestock. The negative impact on social and economic structures may more than outweigh any gains in the long-term rate of production.

A preliminary decision tree is provided in Appendix 1 to assist the assessment of what type of germplasm should be sought for a given situation. Notes on the various steps in the decision tree are given in Appendix 2

The general principles of cross-breeding have been dealt with in the previous chapter and therefore, the details are not repeated here. Many of these details are implicit in our accompanying decision tree, which could also be used when examining the potential use of indigenous germplasm. Additional considerations when examining exotics are whether or not the exotic might be used as a pure-bred and if used in cross-breeding, is it feasible or desirable to maintain a pure-bred exotic population as part of that cross-breeding programme?

Other important considerations are how the exotic germplasm, as pure-bred or cross-bred, will be evaluated. That is dealt with later, but decisions there may impact decisions here. The decision tree suggested here is used to assess likely end uses of hypothetical exotics with identified characteristics based on the assessments of the production environment in Section 1. The process should be repeated once a specific exotic source has been identified and characterised to make sure that the original decisions on the breeding programme still make sense.

We have worked with many of the same assumptions as in the preceding chapter. We do not believe that cross-breeding programmes that involve maintenance of pure-bred stock, either for terminal crossing or rotational crossing have any likelihood of success where any or several of the following apply: a) livestock is an important part of economic and social capital; b) production is by small holders with little infrastructure support; c) marketing and distribution networks for sale of livestock products are not highly developed; d) the lifetime reproduction rate is below three to four progeny per female; e) it is expensive or impossible to maintain pure-bred stock because of lack of adaptation to the local environment. In addition, it is probably not sensible to consider such cross-breeding structures if social, political or climatic fluctuations or the risk of war might periodically disrupt infrastructure support and marketing and production structures.

The above restrictions mean that in the vast majority of cases of low input systems and probably in most medium input systems, the choice will be between the use of the exotic as a pure-bred or in creation of a new composite or synthetic stock. Complementarity of breeds is not relevant when considering synthetics, so the problem is to determine the expected performance of the synthetic based on expected heterosis and proportion of genes from each breed source and then comparing that to the pure-bred performance.

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## **2. Choosing between pure-breeding and various cross-breeding systems**

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When assessing performance, the breeding objective needs to have been defined clearly. Thus, apart from the various performance measures, such as milk yield, growth rate, egg production, etc., there must be an overall definition of economic value within the social, economic and management system in which the new germplasm is to be used. In low to medium input systems, fitness traits such as survival and reproduction rate will often be the key determinants of overall economic value. These traits are often much more difficult to measure than standard performance traits, but they cannot, as is too often the case, be ignored because of that. The problem of assessing fitness traits will be more fully dealt with in Section 5.

In low to medium input environments it is unlikely to be worth the expense and risk of trying to capture heterosis of an exotic cross, unless performance is increased by at least 20 percent. The body of evidence shows that substantial heterosis can generally be expected only for traits closely related to fitness, such as reproduction, stress tolerance and resistance to parasites and disease. The worse the environment, the greater the importance of fitness traits and the greater the heterosis that can be expected. In very stressful environments, substantial heterosis will be observed for production traits such as growth and milk or egg production, because heterosis for fitness traits creates a healthier, stronger animal that is then more able to express its genetic potential for production. This has implications for an efficient testing of germplasm (see Section 4). It also means that if an exotic has sufficient fitness to resist disease, survive stress and reproduce well in the local environment, it is unlikely that a synthetic would do better than a pure-bred exotic (see Appendix 3 for an illustration of the impact of fitness traits).

The degree of heterosis maintained in a synthetic will depend on the cause of the heterosis. Apart from the usual considerations of dominance versus epistasis as the cause (see previous chapter), heterosis due to only one or two genes may cause problems. It is possible that some instances of disease or parasite resistance may be due to a single gene. In many (probably most) cases the gene for resistance can be expected to be dominant, so that the  $F_1$  with an exotic not carrying the gene will exhibit good resistance (and thereby heterosis for production and survival). One quarter of the  $F_2$  will be homozygous susceptible and will exhibit very low, perhaps zero fitness. Production of remaining animals would therefore have to be more than 33 percent higher than the indigenous pure-bred before any gain is made. Such problems would be less severe where resistance is polygenic, as all animals in the  $F_2$  would be expected to have at least some level of resistance. Thus, at this stage of evaluation, some thought needs to be given to the likelihood that one or more key fitness characteristics of the indigenous stock might be controlled by only one or two genes.

Having identified the characteristics desired of exotic germplasm, decisions must be taken on which of the many possible sources of exotic germplasm should be imported and tested. The principal criteria for such decisions will be: a) the likelihood that a given exotic has the desired genetic characteristics; and b) the logistical difficulties of obtaining and importing that exotic. The natural tendency is to consider the logistical difficulties first and then examine genetic characteristics of exotics that would be easy to access. However, a greater chance of genetic improvement will come from first producing a list of potentially useful exotics based on genetic characteristics. Final choices among exotics can then be made based on logistical difficulties. Stocks with the greatest potential will be worth taking more trouble to obtain and import than lower ranking stocks.

Assessment of genetic potential ideally should be based on information that is *sufficient*, *relevant* and *reliable*.

**3.1.1 Sufficiency of information.** For information to be sufficient, it should encompass all characteristics that will determine the value of the stock. This means having information on all performance and fitness traits that will contribute to economic and social value. In general that requires very detailed experiments, trials or performance and life history recording programmes to be in place.

**3.1.2 Relevance of information.** Relevance here is the need for information to be available on performance of the stock in environment and management conditions that match those of the importing country. For information to be fully relevant, all important aspects of the environment and management should match that in the importing country. In most cases, the information available will be only partially relevant, with not all components of the environment and management matching that of the importing country.

**3.1.3 Reliability of information.** Reliability of the information is determined by the statistical accuracy of the experiments, trials, surveys or reports from which information on genetic potential is derived. It is also determined by the credibility of the sources of the information, the methods used to collect the information and how well described are the conditions in which the information was collected. The degree of reliability required will depend on the size of differences between stocks that are expected to be useful. Thus, for example, if one is looking for increases of performance of 100 to 200 percent, information can have relatively low accuracy and yet remain certain that a large difference does exist. If one is looking for improvements of, say, 20 percent, the information will need to be very accurate (see Appendices 5.1 and 5.2, for more detailed statistical arguments on accuracy of estimates of performance characteristics).

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### 3. How to choose among alternative sources of exotic germplasm

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#### 3.1 Evaluating genetic potential of exotic stocks

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It is clear that only very rarely will existing information meet all criteria for sufficiency, relevance and reliability. Stocks in commercial production in developed countries will often have reliable information available and in some cases also sufficient information. However, in most cases the production systems will differ markedly from the low to medium input systems of the importing country, so that the information will only rarely be fully relevant. Conversely, most stocks in low to medium input systems occur in underdeveloped countries, so that while information on such stocks might often be relevant it will rarely be fully sufficient or reliable.

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### 3.2 Sources of information

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Appendix 4 lists the possible sources of information on genetic potential of exotic stocks. In general, electronic access to the research literature is improving rapidly and this provides much more rapid and efficient screening of the information available. A limitation is that electronic access to literature will generally exclude the early literature. Few electronic databases go back beyond the early 1970s and many only go back to the mid-1980s or even later.

An important point is that only a small proportion of the world's sources of livestock germplasm has been properly evaluated. There is a serious bias in the published literature because a publication on one promising breed or stock will spur other groups to study the same breed. Similarly stocks that are already common are more likely to be studied than rare stocks. The result is that a small proportion of the world's germplasm sources dominates the published literature. Thus, while the published literature is a very powerful resource in the search for suitable germplasm, ignoring more anecdotal sources of information would cause exclusion of the majority of germplasm from consideration. Unsubstantiated reports should probably be given much less weight than fully documented assessments of performance, but very promising stocks should be examined more closely, whatever the first source of information.

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## 4. How to import germplasm

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We have not included a decision tree here, but have summarised a variety of options that are available, some logistical considerations for each and some advantages and disadvantages. From this it should be possible to determine the most viable option in each case.

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### 4.1 Import live animals

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This may be a viable option when a pure-bred stock is required on site as a foundation for cross-breeding. The **advantages** of this approach are: a) it is technically fairly easy; not requiring advanced reproductive technologies; b) it can be relatively cheap for very small species such as chickens and rabbits, especially if they can be transported when very young, as is the case with chickens; c) if pure-bred females are imported, a pure-bred herd can be established immediately. There are serious **disadvantages** with this option: a) it will be moderately to very expensive for large animals such

as pigs, goats, sheep and cattle; b) it can sometimes be logistically difficult to guarantee the feed and water supplies of live animals in transit; c) if disease is a problem, imported animals will have no opportunity to acquire immunity and may well succumb. Even where vaccines and/or prophylactic treatments are available for major diseases, a variety of less well characterised and often sub-clinical infections may severely debilitate newly imported exotics; d) animals reared in benign conditions in their home country may not thrive when moved to harsh conditions. A period of careful acclimation may be necessary for imported animals; e) imported animals may be carriers of exotic diseases or parasites and thereby put indigenous livestock at risk; and f) veterinary health laws may prohibit such imports.

A reasonable option for poultry at relatively low cost and fairly low risk of disease if purchased from a reputable company or other agency, but substantial disease risk otherwise. Nevertheless, for poultry this will very often be the least expensive, lowest risk option.

In some species it is technically feasible to consider importing oocytes and then fertilising them *in vitro*, culturing the embryos and subsequently transferring to recipient females. Using this approach one could produce either pure-bred progeny or cross-bred progeny. In the former case, however, it seems preferable to import embryos and in the latter case semen, since these technologies are easier they are generally cheaper than oocyte technologies. At current cost rates, success and technical difficulty, it is difficult to see that import of oocytes would be the desired option.

Import of embryos is a viable option for bringing in pure-bred exotics of cattle, sheep, goats, pigs and rabbits. There are several **advantages** of importing embryos: a) transport costs are low; b) disease risk can often be substantially reduced when compared to live animal imports by use of embryo washing procedures; c) progeny are born to indigenous dams and will acquire immunity to some local diseases via colostrum and opportunity for infection leading to immunity in early life; and d) being born into harsh conditions provides a better opportunity for adaptation than being imported in later life. There are also several **disadvantages** of importing embryos: a) it requires embryo transfer technology to be available in both the exporting and importing country. These technologies require a certain minimum infrastructure to be present, although that infrastructure need only be temporary if a one-time import is made; and b) veterinary health laws may prevent such imports in some cases. Provided that technical and disease problems can be overcome, this will often be the import method of choice for large ruminants and possibly also for pigs and rabbits.

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#### 4.2 Import fertilised eggs

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#### 4.3 Import oocytes

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#### 4.4 Import embryos

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#### **4.5 Import frozen semen**

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Import of frozen semen is a viable option for most ruminants and rabbits. It may also be viable for pigs but success rates may be low. The **advantages** of this approach are: a) transport costs are very low; b) collection is relatively easy; c) delivery is fairly easy; d) disease risks are minimised; and d) progeny will be born to indigenous dams and will acquire immunity to local diseases through colostrum and early life infection leading to immunity. There are some **disadvantages**: a) the progeny will be cross-bred, which will mean that several generations of importation and crossing will be required if a nearly pure-bred exotic population is required. If non-genetic adaptations to disease or environment, or lack of embryo transfer technologies are issued, import of frozen semen may nevertheless be the best way of establishing a (nearly) pure-bred population; b) a certain level of expertise and infrastructure is required, although this can be imported if a one time import is made; c) disease risk is not eliminated; and e) fertility may be lower than with natural mating or use of fresh semen.

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#### **4.6 Import of fresh semen**

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Import of fresh semen will usually be an option for any species for which frozen semen is an option and can be considerably more successful for some species, such as pigs. The **advantages** of this approach are essentially the same as for frozen semen, plus increased fertility in several species. The **disadvantages** are also similar to those for frozen semen, plus the need to deliver semen from the source to the recipient female within the normal shelf life (a few days for most species), plus the need to keep semen in carefully controlled conditions with minimal temperature fluctuations whilst being shipped. Where the technology for frozen semen is available, frozen semen will generally be preferred over fresh semen because of the extended life of the sample and the less stringent handling conditions

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#### **5. How to test exotic germplasm in local conditions**

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The optimum design of a testing programme depends on factors such as: a) the most likely end use of the exotic; b) the principal traits to be evaluated; c) the number of sources of exotic to be tested; and d) the time, financial and technical resources available for testing.

A) The most likely end use of the exotic will generally be dictated by knowledge of the social, economic and production environment and will have been determined before testing begins. In most low input systems, the goal will be some form of synthetic population or replacement with a well adapted exotic, so that testing needs to focus on performance of the synthetic in comparison to existing stock and/or the well-adapted exotic pure-bred. In higher input systems with reasonable infrastructure, terminal (or very rarely, rotational) cross-breeding systems may be feasible and testing will need to be decided between this and a synthetic or a pure-bred indigenous stock or adapted pure-bred exotic.

- B) In all cases the testing needs to evaluate the complete economic and social value of the stock in the relevant environment. The limiting factor in such testing will be the low accuracy of evaluating fitness traits with low heritability, such as fertility, reproduction rate, survival and disease resistance. In low input systems, such traits will often be the principal determinants of the value of alternative germplasm and accurate assessment of these traits cannot be avoided (see Appendix 3 for an example of the impact of fitness traits on overall value). It will often prove very difficult to operate large-scale trials in such conditions. In medium to high input systems, fitness traits may be less of an issue and testing can focus more on production traits, which is generally far cheaper and easier. The risk is that there is a serious fitness problem that is not detected if smaller trials are run. This risk will generally decrease as the input level goes up and the disease problem goes down.
- C) In some cases, choice of exotic will not be obvious before testing commences and it will be desirable, if resources and time permit, to test several exotic stocks. In such cases a hierarchical design should be considered, where several stocks are initially tested at relatively low accuracy, with the poorest performing being sequentially eliminated until one remaining stock is adequately tested.
- D) The time available for testing may have a major impact on design. Crisis situations, such as repopulating after civil war or drought, may allow no time for testing, whereas systems that are currently functioning well will require long and careful testing of alternatives before decisions to introduce new stock are taken. The actual resources available for testing will impact the ability to run trials of adequate size and to record appropriate traits with appropriate accuracy. Where few resources are available, only fairly crude trials may be possible and these will require more cautious interpretation before any decisions are taken. The larger and more detailed the trial, the more confidence can be put in the final decision taking. This principally means that smaller differences will lead to decisions to import exotics into the production system than when only crude trials are possible. This may well determine whether a trial is worthwhile when few resources are available for the trial.

A summary of basic design sufficient for most uses is given here. More details can be found in Appendices 5.1, 5.2 and 5.3, which contains copies of reports by E.P. Cunningham and O. Syrstad (1987) and J. James (1977).

We follow the views of Cunningham and Syrstad (1987, *FAO Animal Health and Production Paper 68*) that it will not be technically feasible to test all possible cross-breeding systems to discover which is the best for any given environment. Rather, it makes more sense to evaluate the additive

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## 5.1 Simple designs

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### 5.1.1 Testing pure-breds and $F_1$

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difference (A) and heterosis (H) between an exotic and an indigenous stock. Once A and H are estimated, the performance of different types and degree of cross-breeding can be predicted. These predictions may be faulty if a large amount of epistasis contributes to heterosis, but errors are unlikely to be large. Moreover, it is expected that the cross that is predicted to be most suitable for the environment will be tested before being launched into widespread application.

The simplest design for estimating A and H involves testing the two parental strains (the exotic and the indigenous stock) and their  $F_1$ . The optimum design is to allocate 34.5 percent of animals to each parent strain and 31.5 percent of animals to the  $F_1$ ; but an equal allocation of animals among the two parents and the  $F_1$  will have nearly the same power. The number of animals required in total to achieve a given accuracy of estimation of A and H are given in the table below. The co-efficient of variation of the trait and the standard error of the estimate of A and H are measured as a percentage of the mid-parent performance. The number of animals required are given for various combinations of co-efficient of variation of the trait and the desired standard error of A and H.

Standard error of A or H	Co-efficient of variation					
	25%		35%		45%	
	A	H	A	H	A	H
2.5	579	468	1 135	918	1 876	1 517
5	145	117	284	229	469	379
10	36	29	71	57	117	95
15	16	13	32	25	52	42
20	9	7	18	14	29	24

Traits will need to be ranked in terms of importance and the size of the standard error that will be required for evaluation. The most important traits will determine the size of the trial. In low input environments, fitness traits will generally be the most important and these will have high co-efficients of variation. The size of the standard error required will depend on the size of differences that are considered important. The exotic pure-bred or cross will generally need to be at least 20 percent superior to the indigenous stock in terms of overall economic merit before replacement is worthwhile. At this lower end, A and H for key traits might be less than 10 percent of the mid-parent mean, requiring small standard errors for accurate assessment. In many cases, however, the expected differences of  $F_1$  and exotic from the indigenous stock will be much larger, allowing somewhat larger estimates of standard errors to be tolerated (see also Appendix 5.3).

In species with low reproduction rates, relatively small differences in survival and reproduction rates will have a large effect on overall value of the stock. In such cases it will often be more efficient to first test an exotic stock for performance traits. Performance traits generally have low co-efficients of variation and in many cases, large expected differences allowing relatively large standard errors to be tolerated. Thus, a preliminary trial of performance traits might require only about 30 to 40 animals. Only if the exotic stock was suitably based on performance traits would a much larger trial for evaluating fitness traits be considered. The second phase trial would probably involve from 500 to several thousand animals.

An important design criterion is that the exotic pure-bred must have had the chance to become fully adapted to the local conditions. This means that they must have been born in the local environment, preferably to dams who themselves were fully adapted. This means testing grand-progeny of live imported animals, or testing pure-breds born after embryo transfer into indigenous locally adapted females. Waiting for production of grand-progeny will be too long a time for large ruminants, but might be acceptable for pigs and poultry, where only a two year delay would be involved.

In many situations the pure-bred exotic will not be available for evaluation. This may be because the exotic does not survive, or fails to thrive, in the local environment. Alternatively, a strategic decision may be taken that it is not worth the expense and difficulty to import, establish and then test the pure-bred exotic if it is unlikely that the pure-bred exotic would be required as part of the cross-breeding programme. In such cases, A and H can still be estimated by including  $F_2$  and backcross animals in the design. To obtain the same standard errors of estimates, from 2.5 to 8.3 more animals will be required than when testing both pure-bred parents and the  $F_1$  (see Appendix 5.1 for more details).

In some cases one would not be interested in cross-breeding and the evaluation trial would include only the pure-bred exotic and indigenous stocks. In that case the difference between the stocks is  $2A$ . The number of animals required will be  $2/3$  of the number given in the above table for the appropriate value of A (see also Appendix 5.2 for more details of testing pure-breds).

It was noted in 5.1 that it will often be sensible to first confirm the utility of an exotic for performance traits before testing fitness traits. A similar design can also be used to perform a preliminary screen of a number of possible exotic stocks for general performance characteristics and then test the best one or two stocks for fitness traits. In this case it may be

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*5.1.2 Testing when the pure-bred exotic is not available.*

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*5.1.3 Testing pure-breds only*

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**5.2 Hierarchical designs**

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possible to reduce even further the number of animals required for phase one testing, because relatively small differences among exotic stocks are unlikely to matter greatly.

No calculations have been performed, but an efficient design might look something like the following:

- Phase 1: Evaluate performance traits on approximately 30 animals from each of the several exotic stocks.
- Phase 2: Evaluate the top two or three exotic stocks for fitness traits plus production based on about 400 animals.
- Phase 3: Obtain more accurate estimates of fitness traits on best exotic stock based on about 1 500 animals

Phase 3 might be replaced by a direct test of the synthetic or other cross-bred thought to be the best option based on results in Phases 1 and 2.

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### 5.3 More complex designs

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Based on Larry Cundiff's/MARC experience

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## 6. How should the final cross-breeding system be put together and operated?

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Most of the issues relating to constructing and maintaining a cross-breeding programme have been dealt with in the previous chapter. The only novel problem posed by exotics is if the maintenance of a pure-bred population is required and pure-bred animals do not thrive in the local environment. In most cases a pure-bred exotic population would be used to supply males for use in cross-breeding. Thus at the very least the males must be able to survive and breed successfully in the local environment or the use of AI must be a feasible option. In the former case, the exotic can be treated as any other pure-bred population, albeit with potentially more expense and greater difficulty involved. In the latter case, the population might be maintained in a more benign environment with semen shipped into the production environment. Alternatively, the choice might be to continuously import semen from another country, with its attendant disadvantage of continuous expenditure of foreign exchange. In low input environments, however, use of AI is very unlikely to be feasible, so that any cross-breeding system that requires use of poorly adapted pure-bred exotic males in the main production system will also not be feasible.

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## Appendices and attachments

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**Appendix 1** Decision Tree 1: Identifying likely role of an exotic.

**Appendix 2** Notes to Decision Tree 1.

**Appendix 3** Example of effect of fitness on decisions among pure-breds and cross-breds.

**Appendix 4** Sources of information on exotic stock characteristics.

**Appendix 5.1** Cunningham and Syrstad FAO chapter.

**Appendix 5.2** John James' report of testing groups.

**Appendix 5.3** John James' arguments on size of differences needed.

## Appendix 1.1 Decision tree for deciding on requirements for and broad uses of exotics

Assessment	Decision
1: Is there a need for improved ability to survive a harsh environment that might realistically be found in exotic germplasm (e.g., improved heat and drought tolerance or disease resistance)?	<b>Yes:</b> go to 13 <b>No:</b> go to 2
2: Are there extra nutrition and/or management resources available to sustain production above current levels?	<b>Yes:</b> Go to 3 <b>No:</b> Go to 4
3: Are the extra resources available at all times or are there periods when there are no or very little extra resources (e.g. periodic drought, erratic supply of supplements due to poor infrastructure or political and economic instability).	<b>Constant supply:</b> go to 5 <b>Erratic supply:</b> go to 6
4: Do not seek exotic germplasm. Examine possibilities of a within breed selection programme or cross-breeding programme based on indigenous stocks.	
5: Define the expected level of production that could be supported with the extra resources available in an average year. Express as a percentage of current production levels.	<b>&gt;200%:</b> go to 9 <b>120–200%:</b> go to 10 <b>&lt; 120%:</b> go to 4
6: Define the worst case scenario for resource inputs. Are animals with a production potential which is higher than that of the current animals likely to survive and then recover from the worst case scenario better or worse than current animals? Define survival and recovery as greater than or less than that of current stock.	<b>Greater than:</b> go to 5 <b>Less than:</b> go to 7
7: Does this species have major importance as a form of economic and social capital?	<b>Yes:</b> go to 9 <b>No:</b> go to 8
8: Based on the reproductive capacity of the species and the production potential when extra resources are available and on projected frequency of episodes of low resource availability, calculate the long-term production of the exotic as a proportion of the current stock.	<b>&gt;200%:</b> go to 10 <b>120–200%:</b> go to 11 <b>&lt; 120%:</b> go to 4
9: Is there a substantial risk of much lower survival of exotic germplasm such that either the mean of long-term economic and/or social capital might be substantially reduced or its variance substantially increased.	<b>Yes:</b> go to 4 <b>No:</b> go to 8
10: Does the local environment require environmental and/or disease stress tolerance already available in indigenous germplasm?	<b>Yes:</b> go to 11 <b>No:</b> go to 12

(To be continued...)

(...To be continued)

<p>11: Seek a moderate production exotic germplasm with potential for adaptation to the local production environment and use as a pure-bred or high percentage (75 percent exotic genes) cross or synthetic. Or, seek a high production exotic germplasm with some potential for adaptation for use in a moderate to low percentage (<math>\leq 50</math> percent exotic genes) cross.</p>	<p>Go to decision tree 2</p>
<p>12: Seek high production exotic germplasm with the potential for adaptation to the local production environment and use as pure-bred or a <math>\frac{3}{4}</math> or higher cross or synthetic.</p>	<p>Go to decision tree 2</p>
<p>13: Go to 2 and determine how much room there is for improved production assuming that the exotic would bring existing levels of survival to the local environment at times when extra resources are available. You should end up at box 4, 11 or 12.</p>	<p><b>If box 4:</b> go to 14  <b>If box 11:</b> got to 15  <b>If box 12:</b> got to 15</p>
<p>14: Seek exotic germplasm with moderate to low production capability and higher ability to thrive in the local environment than existing stock.</p>	<p>Go to decision tree 2</p>
<p>15: Determine whether a cross-bred of indigenous stock to exotic germplasm with high production potential could have higher production than an exotic germplasm with high stress tolerance used as a pure-bred or as a cross-bred with indigenous stock. Express result in terms of the production potential in the local environment of the high production versus the high stress tolerant exotic germplasm.</p>	<p><b>Higher:</b> go to 11  <b>Similar:</b> go to 11 and 14  <b>Lower:</b> go to 14</p>

Numbers refer to decision item in the table. Subscripts (a or b) to numbers refer to a) the basis of the decision; or b) the actual cut-offs used.

**General notes:** In these decision trees, exotic refers to any source of germplasm that is not indigenous to the region in consideration. The evaluations here are intended to define the limits of production capability and lead to broad definitions of what type of exotic germplasm might be sought. The same decision tree could, however, be used when a specific exotic or indigenous stock is being considered.

**2a:** Production in any system can only increase over the current production levels if extra nutritional resources are available or can be made available for the livestock. These resources might be available through increased efficiency of utilisation of a new stock, but differences between stocks will generally be fairly small and will tend to favour genotypes with high stress tolerance and low productivity. Thus, if importation of new germplasm is to be considered, there will need to be additional feed resources not currently being utilised. In order to access these feed resources, additional management resources may be required. These might be as varied as the manpower or transportation to bring crop residues to the livestock, the development of a complex infrastructure to produce crops specifically for livestock production, the use of prophylactics to protect against disease, the provision of water and shelter in harsh environments, or the development of marketing systems to allow surplus production to be sold.

**3a:** *A chain is only as strong as its weakest link.* Success in low to medium input livestock production systems is often less related to their ability to produce surpluses in times of plenty than their ability to survive times of scarcity. The production environment should therefore be evaluated in terms of both average resource availability and the frequency and severity of periods of low resource availability.

A characteristic of many low input environments is their variability over time, with periodic episodes of very low availability of feed and/or water, generally due to drought. Resource availability is often also compromised by human factors such as political and social upheaval, fluctuations in world commodity prices and war.

**3b:** Erratic here is defined as fluctuations in resource supply that would cause the lowest level of resource availability to be as low or lower than the average utilised by the current stock. The answer should be erratic if there is any likelihood of one or more episodes of such low resource availability in the foreseeable future (say 30 years).

**5a:** The calculations required here are theoretical. They require an assessment to be made of the nature and level of nutrients that could be utilised if a suitable genotype was found. These can then be compared to the estimates of current nutrient utilisation to determine the level of

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## Appendix 2. Notes on decision tree for deciding on requirements for and broad uses of exotics

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production that could be supported. When making such calculations allowance should be made for the observation that high output genotypes invariably have higher maintenance requirements than low output genotypes. This will have implications for both the average level of production and the ability of the genotype to thrive under low input episodes (this is relevant to question 6).

Provided that information is available on nutrient type and supply, approximate estimates of maximum production capacity can be made based on livestock nutrition guidelines such as those produced by the National Research Council of the USA and the Agriculture and Food Research Council of the UK, etc. Not all feedstuffs will be covered by such guidelines, but in most cases prediction formulae can readily be amended to deal with feedstuffs of different composition to those covered in the various guidelines. Note that the objective here is to obtain a rough guide to the level of production that might be possible rather than the highly accurate estimation that is usually sought in highly intensive production environments.

One key element in many tropical environments, not present in most temperate environments, is the presence of toxic plants that could have severe effects on production of livestock not adapted to local conditions. This should generally be ignored here when estimating production potential, but should be noted as a highly important criterion when evaluating the need for traits of adaptation to the local environment (question 10).

**5b:** The cut-off of 120 percent is relatively arbitrary, but it is deemed unlikely that it would be desirable to implement a programme for importing, testing and application of an exotic for less than a 20 percent gain in productivity. Getting to the application of an exotic has many costs involved and is never totally without risk of failure due to unforeseen circumstances when compared to a tried and trusted indigenous stock. In many cases the cut-off should probably be higher than 20 percent; it may be lower in cases where relatively high levels of input and infrastructure are available and fluctuations in resource availability are low.

**6a:** In general, animals with high production potential will also have high maintenance requirements and this will affect their ability to survive and reproduce in times of low resource availability. Similarly, high production genotypes may not have the same ability to digest high roughage/low nutrient density diets, which may compound the problem of requiring higher inputs for maintenance.

In some cases the extra resources that allow higher production will include such things as availability of prophylactic treatments to allow disease susceptible genotypes to thrive in the local environment or provision of water and housing to alter the physical environment. If any of this

management support is unavailable in part or whole from time to time, the evaluation here should include what would happen to the high production germplasm if such support was removed.

The evaluation can be a fairly subjective assessment of whether or not it is likely that the exotic would suffer worse losses and take longer to recover than the current stock. The answer should err on the lower side of survival and recovery if there is any doubt, so that the decision tree goes on to an explicit evaluation of the impact of reduced survival and recovery. There are cases, however, where it might be expected that higher production genotype might suffer marginally worse losses than indigenous stock during low resource episodes but would be expected to rebuild population sizes more rapidly (because of high reproduction potential). In such cases their combined survival and recovery might be considered superior to that of the indigenous stock.

**7a:** The use of livestock as social and/or economic capital is extremely important in many societies. In such cases, the long-term production capability may be of less importance than ability to maintain or increase numbers of livestock maintained by family or other social groups. If a change in germplasm significantly alters the risk of some groups losing their capital holdings, this could lead to social change that would outweigh any benefits from increased long-term production potential of the livestock system.

**8a:** It can safely be assumed that for species such as cattle and sheep, reproductive rates in a low to medium input environment will be low and recovery from population reduction will be slow. Species such as pigs, poultry, ducks and geese will make much more rapid recoveries and can sustain more severe losses and still make rapid recovery to full population size and production levels when favourable conditions return. Calculations of expected net productivity of exotic versus current stock can be made based on the expected frequency and severity of periods of low resources in relation to the species reproductive rates and potential production levels during good years of the higher production genotype.

The following is a crude example of such a calculation that nevertheless may work well as a first approximation in many situations.

It is assumed that the current stock survives the low resource periods with no loss of population size, but neither does the current stock or the exotic produce any surplus (product) during the low resource period. The exotic also has no surplus while population size is being rebuilt to that required by the production system.

The long run production of the exotic expressed as a proportion of the current stock is,

$$\text{long run production of exotic} = y^*(T - t - n)/(T - t),$$

where  $y$  is the production of product (an identified single product or an aggregate net economic benefit) of the exotic in good years expressed as a proportion of the production of the current stock;  $T$  is the total cycle length (the period in years between episodes of low resource availability);  $t$  is the length in years of the average episode of low resource availability;  $n$  is the number of years it takes the exotic to recover its population size and is given by,

$$n = -\log(p)/\log(r)$$

$p$  is the proportion of the original population that survives the period of low resource availability; and  $r$  is the annual rate of population growth of the exotic during periods of good resource availability.

The result of the production calculation is clear. Exotics will produce more than indigenous provided the rate of production is more than sufficient to overcome the years of lost production while population size recovers. This becomes more unlikely as the time between episodes of low resource availability goes down, the reduction in population size of the exotic becomes more severe and the reproductive rate and hence rate of population growth goes down. Species with high reproductive rates, such as pigs and poultry, have a much greater potential to bounce back from periods of low resource availability than species with low reproductive rates such as cattle and sheep.

The above estimate of production tends to favour the indigenous stock, because it does not account for products being produced by the exotic during the expansion of the population phase. It will be a disadvantage to the indigenous stock if they can produce products during periods when exotics produce nothing or are reducing in population size. More complex estimates of total production can be constructed that allow for these and many other more realistic assumptions.

It is important to note that the production calculation does not account for use of livestock as economic and/or social capital, where the existence of a live animal has substantial value irrespective of whether or not it is currently producing anything. In such cases the loss of some or all livestock owned by a proportion of families or other groups would cause a much larger economic loss than indicated above. Here we deal with that at a separate point in the decision tree, but it would be preferable to find a way of modifying the product calculation to include the concept of economic and social capital.

**8b:** see 5b

**9a:** A careful economic and social appraisal should be carried out where livestock form an important source of economic and social capital and where new germplasm might have lower survival than current stock during low resource episodes. The important question is whether the average long-term economic/social capital might be reduced, or if the variance might be increased and in either case by how much. Reduction in the average capital may be easier to understand and even estimate than the variance. In many cases the average reduction will be a simple, probably linear function of long-term average reduction in number of animals. The possibility that exotic germplasm might actually increase long-term capital should also be considered. Change in the variance of economic/social capital could well be more important than change in the mean. Increased variance would cause a proportion of livestock owners to lose their capital, leading to concentration of capital in fewer hands. This could have profound implications for social structure and distribution of wealth in rural communities.

The choice here is put in terms of substantial negative effect on economic/social capital versus little negative, null or positive effect on capital. If a substantial negative impact or substantial risk of such impact is anticipated, exotic germplasm with high production potential should not be considered. No explicit framework is proposed here for estimating these impacts on economic/social capital. Future versions should include such frameworks and might lead to a more objective balance being defined between long-term productivity and variance in social capital.

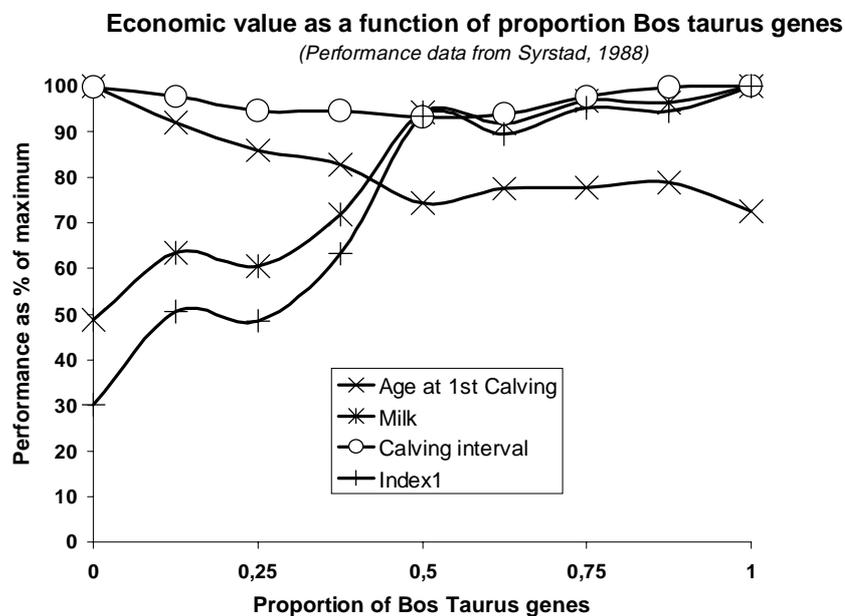
**10a:** Elements to be considered here include heat, parasite and disease tolerance, strong foraging ability, ability to digest toxic plants without severe ill effects and ability to survive periods of severe resource restriction.

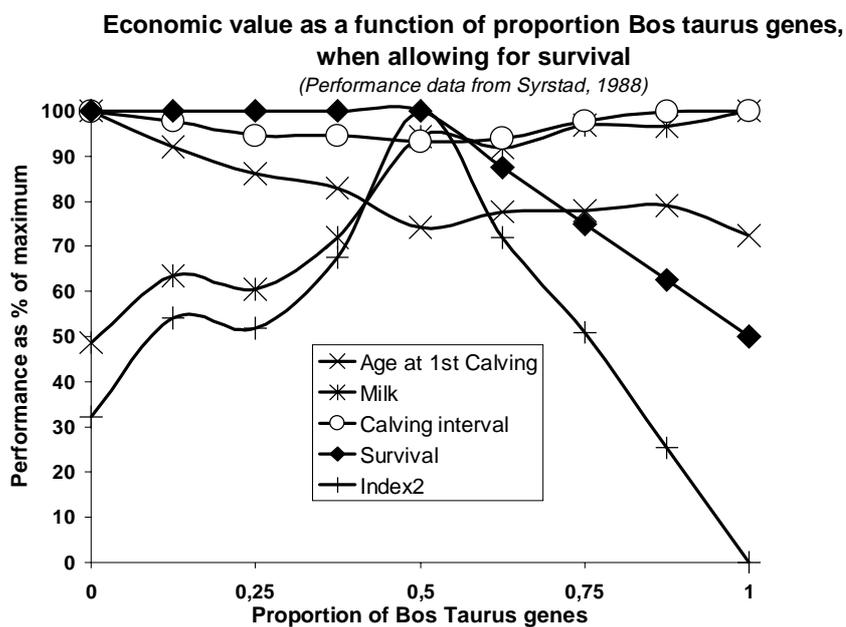
**Appendix 3.**  
**An example of**  
**the effect of**  
**fitness on**  
**value of and**  
**choice**  
**between**  
**pure-bred and**  
**cross-bred**  
**stock**

The impact of fitness, specifically survival, on the overall assessment of value of various cross-bred stock is given in the following figures. In both figures, age at first calving, calving interval and milk yield are plotted against proportion of *Bos taurus* genes. Data is the average of many global studies as summarised by Syrstad (1988). Values are expressed as a percentage of the maximum for the trait.

In the top figure, it is assumed that overall economic value can be derived as Index 1 = Milk - ¼ age at first calving - ¼ calving interval, with each trait expressed as a percentage. Index 1 is then also expressed as a percentage of its maximum value. In this hypothetical situation, there is little to choose between the F<sub>1</sub>, the pure-bred *Bos taurus* and any degree of backcross to *Bos taurus*.

In the lower figure, values for survival have been added. Although these are hypothetical values in this case, they could easily represent something close to reality in a very harsh or disease prevalent environment. It is assumed that the system is not viable (has no value) when survival falls to 50 percent. Allowing for differences in survival, overall economic value is now expressed as Index 2. In this situation, there is a very clear advantage of the F<sub>1</sub> over all other cross-breds and pure-breds. This contrasts markedly with the situation in the upper figure, which implicitly assumes that survival of all genotypes is the same. The need to record fitness traits such as survival is clear and cannot be avoided just because it is difficult to do so.





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## **Appendix 4. Sources of information on characteristics and status of exotic germplasm**

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### ***Research papers***

Animal Breeding Abstracts, published by C.A.B. International provides by far the oldest and most comprehensive routes into the published literature on livestock genetics, including breed evaluation, comparisons and cross-breeding trials. Information in A.B.A from 1972 to the present can also be accessed electronically (see search engines below).

### ***Publication Series***

Bulletin of Animal Genetic Resources Information. Published free-of-charge by FAO, Viale delle Terme di Caracalla, I-00100 Rome, Italy. Also available in the Library of DAD-IS at URL <http://www.fao.org/dad-is/>

### ***Books***

Mason, I.L., 1996, A world dictionary of livestock breeds, types and varieties., 4th ed. C.A.B. International, Wallingford, Oxford, pp. 273.

### ***Websites and other search engines***

The FAO DADIS website, currently under construction, will eventually contain information on the majority of the world's livestock breeds, with search engines allowing rapid search for particular breeds, regions or traits. Located at <http://dad.fao.org/dad-is/>

The International Livestock Research Institute (<http://www.cgiar.org/ilri>) is also developing a Domestic Animals Genetic Resources Information database (DAGRID), but this, at the time of writing, was not yet available.

Most scientific literature databases now provide electronic search capabilities. The two most useful are AGRICOLA and the C.A.B. Animal Breeding Abstracts. These databases are accessible to paying subscribers, but most university libraries in developed countries will provide access for their staff, students and collaborators. The National Library of Agriculture of the USA also maintains a free access AGRICOLA database and search engine at <http://www.nal.usda.gov/ag98/ag98.html>. Electronic access to CAB abstracts dating back to 1972 is provided by a number of different service providers (for a fee). Details can be found at <http://www.cabi.org/>

Publications dealing with animal disease resistance and susceptibility and most aspects of genomics and gene discovery are increasingly being covered by MEDLINE. Two good points of access are <http://www.biomednet.com/db/medline/> and <http://www.ncbi.nlm.nih.gov/PubMed/> The former site allows direct downloading of references into several electronic reference manager software packages that can be very useful for building databases on particular topics.

General web search engines such as Netscape Search (formerly Yahoo) at <http://search.netscape.com/> will sometimes turn up useful information on specific breeds or traits that is not easily found through other means. Such information is rarely verified by independent review and is often placed by individuals or organizations with vested interests. Nevertheless an increasing amount of truly useful information can be found by this means.

## Appendix 5.1

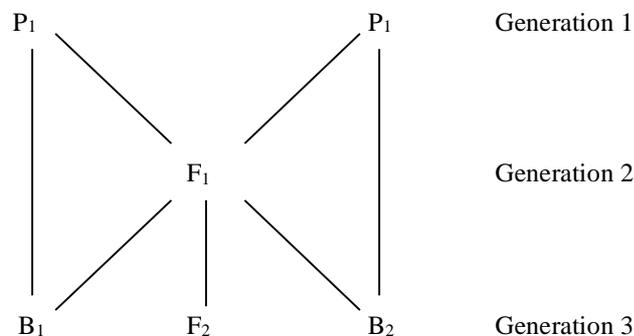
Chapter 6 of E.P. Cunningham and O. Syrstad, 1987. Cross-breeding *Bos indicus* and *Bos taurus* for milk production in the Tropics. FAO Animal Production and Health paper. No.68

The contemplation of cross-breeding with *Bos taurus* breeds in a *Bos indicus* population is based on the initial presumption that sufficient additive genetic difference (A) exists between the local and exotic breeds and/or sufficient heterosis (H) is exhibited in crosses between them, that some form of cross-bred animal will be more productive than the local breed. Unless these additive and heterotic effects can be accurately estimated in advance, there is great difficulty in deciding what the appropriate breeding strategy should be. Depending on the absolute and relative values of A and H, the best strategy may be any of the following: breed replacement, some form of synthetic, rotational crossing, or up-grading to half or three-quarter exotic.

It could be enormously expensive for a country to discover the correct strategy by trial and error. The time lost in pursuing inappropriate strategies could run into decades. The delay in achieving possible increases in productivity could be very serious economically. The scale of some animal populations and the ease with which inappropriate cross-breeding schemes can be introduced via AI, mean that very widespread disappointment, confusion and economic loss could result from unguided cross-breeding.

All of these considerations serve to strongly emphasise the necessity for well-planned trials at the beginning of such a cross-breeding programme and to provide an adequate information base on which to design the subsequent cross-breeding strategy. Considerable care and investment is justified in the design and conduct of these trials because of the scale, duration and economic impact of the breeding programmes which follow.

The primary purpose of any such cross-breeding trial is the estimation of A and H with sufficient accuracy and precision for subsequent plans to be developed with reasonable confidence. If such trials are to be conducted within the first two generations of crossing between the two breeds, they can involve any or all of six generation groups: the two parental breeds, the F1, F2 and the backcrosses of the two parental breeds. These six groups are as follows:



A and H can be estimated from the differences between these groups. It is assumed, of course, that the trial is conducted in such a way that the differences between the groups are not a reflection of environmental, time, location and nutritional or other non-genetic factors. In order to obtain estimates of both A and H, a minimum of three of these groups is required in the trial. Starting with the local population (P1), it is relatively easy to generate F1 offspring using imported semen or males. It may also be possible to provide some animals of the exotic breed (P2) for evaluation in the same environment. This combination of three groups (both parents and F1) is the most efficient set out of the six possible groups which could be used.

With this optimal set, what size of experiment is required to give an acceptable level of precision in the estimation of A and H? This is the basic question in the design of such trials. Precision is best measured as the standard error of the estimate of A or H. If, for example, the additive difference A is expected to be about 40 percent of the mid-parent mean, an estimate of this with a standard error equal to 10 percent of the mid-parent mean (e.g. one-quarter of the actual value estimated) might be regarded as adequate precision for the use of the estimate with confidence in the development of breeding plans. Similarly, if H was expected to be approximately 20 percent of mid-parent value, then a standard error of 5 percent (of mid-parent value) might be regarded as adequate precision. As the scale of the experiment goes up, the size of these standard errors of A and H comes down. It is then a matter of judgement as to what balance of precision versus scale is acceptable.

Table 1 shows the scale of experiment (with two parental groups and F1) required for given levels of precision for the estimation of A and H. Traits will differ in their inherent variability and this in turn will affect the relationship between precision and scale. Three levels of basic variability are therefore provided for: co-efficients of variation of 25, 35 and 45 percent. To achieve given levels of the standard error of A or H (2.5, 5, 10, 15, 20 percent), the number of animals required in the trial is indicated. In all cases, optimal allocation of numbers to the three groups is assumed.

The following example illustrates the use of the table. If the main trait of interest has a co-efficient of variation of 35 percent and the standard errors of A and H are each required to be no greater than 5 percent, then the experiment should contain 284 animals to give this level of precision for the estimation of A, while 229 animals will achieve the desired precision in the estimation of H. As the design is the same in all cases, H is always more precisely estimated than A (about 20 percent fewer animals being required to give the same precision).

*Table 1. Number of animals required to give specified standard errors (SE) of A or H at different levels of variation. (SE and CV both measured as percent of mid-parent mean).*

Standard Error of A or H	Coefficient of variation					
	25		35		45	
	A	H	A	H	A	H
2.5	579	468	1 135	918	1 876	1 517
5	145	117	284	229	469	379
10	36	29	71	57	117	95
15	16	13	32	25	52	42
20	9	7	18	14	29	24

In these calculations, an optimum allocation of animals in the three groups is assumed. This is defined as an allocation of the total number of animals available in the three groups in such a way as to minimise the sum of the variances of A and H. In the case of this particular design (two parents and  $F_1$ ), the optimum is achieved by allocating 34.5 percent of the animals respectively to the two parental groups and 31 percent to the  $F_1$  group. In the example given above, therefore, the 284 animals in the experiment would be allocated 98 each to the two parental groups and 88 to the  $F_1$  group.

The optimal set discussed above includes only the first two generations (both parents and  $F_1$ ). In the next generation, three groups are possible:  $F_2$  obtained by *inter se* mating of  $F_1$ ;  $B_1$  obtained by backcrossing  $F_1$  to parent 1;  $B_2$  obtained by backcrossing  $F_1$  to parent 2. There can be difficulties in having these three groups comparable to the parental and  $F_1$  groups because they are generated at a later point in time. However, it may be possible to generate further samples of the parental and  $F_1$  groups to give valid comparisons.

Assuming that problems of this nature can be overcome and that all three of these additional groups can be made available, do they contribute to the value of the experiment? One way to respond to this question is to specify a fixed total number of animals in the trial and to reallocate a certain proportion of them from the parental and  $F_1$  groups to the  $F_2$  and backcross groups. We can then observe the effect on the actual standard errors of A and H obtained. The results of this calculation are given in Table 2.

Table 2. The effect on the standard errors of A and H of reallocating resources from parental and  $F_1$  groups to backcrosses and  $F_2$  groups.

Percent of animals reallocated from $P_1$ , $P_2$ & $F_1$ to $B_1$ , $B_2$ & $F_2$ groups	Relative Size of Standard Errors of	
	A	H
0	100	100
10	104	105
20	109	110
30	114	117
40	120	125
50	127	136

It can be seen that for fixed total experimental resources, the inclusion of these extra three groups in all cases reduces the precision of the estimates of A and H. If half of the animals are reallocated, the standard errors of the resulting estimates of A and H are increased by 27 percent and 36 percent, respectively.

In the design of such experiments, it is not always possible to choose the best combination of groups ( $P_1$ ,  $P_2$ ,  $F_1$ ). For example, where  $P_2$  is an exotic breed, it may not be possible to include it for practical or financial reasons. However, semen can be readily imported, so that  $F_1$  progeny are usually easy to produce. From the  $F_1$  generation, it is of course easy to produce  $F_2$ . Backcrosses to the exotic breed can be generated by further semen importations, while backcrosses to the local breed can be produced either by mating  $F_1$  cows to bulls of the local breed, or vice versa.

Table 3 shows the effect on the precision of estimation of A and H of using different combinations of the six possible breeding groups in the experiment. For each design, optimal allocation is again assumed, for example, a distribution of animals over the groups involved in such a way as to minimise the sum of the variances of A and H. The final column gives the relative scale of experiment (for example, number of total animals) required to give precision equal to that obtainable with the optimal design.

It can be seen that in all cases the optimal combination ( $P_1$ ,  $P_2$ ,  $F_1$ ) is considerably more efficient than any other design. The next best design requires at least twice the resources to give the same precision.

*Table 3. Comparison of the precision attainable with different combinations of P<sub>1</sub>, P<sub>2</sub>, F<sub>1</sub>, B<sub>1</sub>, B<sub>2</sub> and F<sub>2</sub> groups. Optimal allocation to groups minimised V(A) + V(H).*

Optimal percent of total animals allocated to groups						Relative size of standard errors of		Relative number of animals needed for equal precision
P <sub>1</sub>	P <sub>2</sub>	F <sub>1</sub>	B <sub>1</sub>	F <sub>2</sub>	B <sub>2</sub>	A	H	
35	35	31	--	--	--	100	100	100
37	23	--	41	--	--	111	191	231
29	29	--	--	41	--	109	188	223
23	37	--	--	--	41	111	191	231
22	--	30	--	48	--	335	214	826
22	--	35	--	--	43	170	145	254
17	--	--	47	37	--	366	385	1 405
26	--	--	46	--	29	198	288	587
13	--	--	--	49	38	360	558	2 111
--	--	19	38	43	--	370	254	1 047
--	--	31	35	--	35	200	200	400
--	--	19	--	43	38	370	254	1 047
28	28	--	22	--	22	102	186	212
27	31	--	--	30	13	108	187	221

## **Acknowledgements**

The collaboration of Dr. John Connolly in Chapter 6 is acknowledged.

Suppose an experiment is carried out as follows in order to detect genotype-environment interactions. A total of  $s$  sires each is tested in  $p$  locations, with  $n$  daughters per sire at each location. We assume sires are randomly chosen, but that specific locations are used. The analysis of the result will be as follows:

Source	D.F.	M.S.	E (M.S.)
Locations	$p - 1$	MSL	$\sigma^2 + n\sigma_{SL}^2 + ns\sigma_L^2$
Sires	$s - 1$	MSS	$\sigma^2 + np\sigma_S^2$
Interaction	$(s - 1)(p - 1)$	MSI	$\sigma^2 + n\sigma_{SL}^2$
Error	$sp(n - 1)$	MSE	$\sigma$

The interpretation of the variance components is obvious. The statistical test at the  $\alpha$  significance level for the presence of interaction is

$$(MSI/MSE) > F_{(s-1)(p-1), sp(n-1), \alpha}$$

the  $\alpha$  point of the appropriate variance ratio distribution. Now, under the assumption that the ratio  $MSI/MSE$  has the distribution of  $(\sigma^2 + n\sigma_{SL}^2)/\sigma^2$  times  $F_{(s-1)(p-1), sp(n-1), \alpha}$ . Thus denoting  $\sigma_{SL}^2/\sigma^2$  as  $1$ , the probability of obtaining a significant result at the  $\alpha$  level is  $\text{Prob} \left\{ (1 + n\Theta)F_{(s-1)(p-1), sp(n-1)} > F_{(s-1)(p-1), sp(n-1), \alpha} \right\}$ . If we specify a value for this probability, which is known as the power of the test, then for a given experimental design we can find, from tables of the F distribution, the value of  $1$  which will give this specified power.

For instance, we may take  $p = 2$  and consider the range of experimental designs with  $s = 10, 20, 40$  using  $\alpha = 0.05$ . We find the values of  $1$  which give powers of 75 percent and 90 percent for each design.

## Appendix 5.2. Detection of sire by location interaction and comparison of groups of sires

by J.W. James  
University of New  
South Wales

Working Paper No. 2. Prepared for the APC Expert Panel  
investigating the Introduction of New Dairy Cattle Genotypes  
into Australia. April 1975.

Minimum values of  $\Theta = \sigma_{SL}^2 / \sigma^2$  which will give significant interactions at the 5 percent level with the specified power

s	Power	n		
		10	20	40
10	75%	0.1953	0.0954	0.0473
	90%	0.3188	0.1552	0.0771
20	75%	0.1122	0.0555	0.0267
	90%	0.1673	0.0820	0.0398
40	75%	0.0704	0.0346	0.0148
	90%	0.0988	0.0480	0.0240

It is of interest to interpret these figures in terms of genetic correlations as follows. If  $r_G$  is the genetic correlation between performance in the two locations,  $h^2$  is the heritability and  $\sigma_p^2$  is the phenotypic variance, then

$$\sigma^2 = (1 - \frac{1}{4}h^2)\sigma_p^2$$

$$\sigma_s^2 = \frac{1}{4}h^2\sigma_p^2$$

$$\sigma_{SL}^2 = (1 - r_G)\frac{1}{4}h^2\sigma_p^2$$

and hence

$$\Theta = \frac{(1 - r_G)h^2}{4 - h^2}$$

or

$$r_G = 1 - \frac{4 - h^2}{h^2}\Theta$$

For a known  $h^2$ ,  $r_G$  values can then be converted to genetic correlations. We do this taking  $h^2 = \frac{1}{4}$  so that  $r_G = 1 - 15\Theta$ . We then obtain the following table, which is simply the preceding one in a different form.

Maximum values of  $r_G$  when  $h^2 = 0.25$  which will give significant interactions at the 5 percent level with specified power

s	Power	n		
		10	20	40
10	75%	-1.93	-0.43	0.29
	90%	-3.78	-1.33	-0.16
20	75%	-0.68	0.17	0.60
	90%	-1.51	-0.23	0.40
40	75%	-0.06	0.48	0.78
	90%	-0.48	0.28	0.64

Genetic correlations less than -1 are of course impossible, but the corresponding 1 values may be of some use when all of the conditions specified in deriving the results do not hold. It may be noted that for a given total number of daughters, a lesser degree of interaction may be detected by using many daughters of few sires than can be detected with few daughters of many sires. Thus, with 400 daughters per location, the use of ten sires each having 40 daughters enables interaction to be detected with 75 percent power if  $\lambda$  is 0.0473, but  $\lambda$  must be as large as 0.0704 if we use 40 sires each with ten daughters.

It is also worth noting that if only highly selected sires were used in such a trial, the power would be reduced. The reason is that  $\Phi^2$  would be unaffected, but  $\sigma_{SL}^2$  would be reduced because there would be less variation between sires than when sires are randomly chosen. For the same reason, the power of the test for interaction could be increased by using a combination of very good and very bad bulls, though this may be an unattractive proposition.

Now suppose that in this experiment half of the sires are from one genetic group and half are from another and we wish to compare the two group means. We assume that either there is no sire by location interaction, or we are interested in the average genetic value over both locations.

The variance between sire means within a group is  $\sigma_s^2 + \sigma^2/np$ . There are  $\frac{1}{2}s$  sires in each genetic group, so the variance of a group mean is

$\frac{1}{\frac{1}{2}s}(\sigma_s^2 + \sigma^2/np)$  and the variance of the difference between group means

is twice this or  $\frac{4}{s}(\sigma_s^2 + \sigma^2/np)$ . With  $p = 2$ , this may be rewritten as

$$\sigma_p^2 \left[ \frac{h^2}{s} + \frac{2 - \frac{1}{2}h^2}{sn} \right].$$

Now a difference is significant at the 5 percent level if  $D > 1.96\Phi_D$ , where  $D$  is the difference between means and  $\Phi_D$  is its standard error. If  $\mu$  denotes the true mean difference, the chances are 90 percent and 75 percent that  $D > \mu - 1.28\Phi_D$  and  $D > \mu - 0.67\Phi_D$ . Thus for powers of 75 percent and 90 percent, we need

$$\mu \geq (1.96 + 0.67)\Phi_D \text{ and } \mu \geq (1.96 + 1.28)\Phi_D$$

or

$$\frac{\delta}{\sigma_p} \geq \begin{cases} 2.36 \\ \text{or} \\ 3.24 \end{cases} \sqrt{\frac{h^2}{s} + \frac{2 - \frac{1}{2}h^2}{sn}}$$

Minimum genetic differences between groups in standard deviation units which give significant differences at the 5 percent level with specified power

s	Power	n		
		10	20	40
10	75%	0.55	0.49	0.45
	90%	0.68	0.60	0.56
20	75%	0.39	0.34	0.32
	90%	0.48	0.42	0.39
40	75%	0.28	0.24	0.23
	90%	0.34	0.30	0.28

Again using the value  $h^2 = 0.25$ , we find the condition

$$\frac{\delta}{\sigma_p} \geq \left\{ \begin{array}{l} 2.36 \\ or \\ 3.24 \end{array} \right\} \sqrt{\frac{1}{4s} + \frac{15}{8sn}}$$

Values of this criterion have been calculated for the range of values of s and n used before and are shown in the table. Since the co-efficient of variation of milk production can be expected to be about 20 percent, these figures can be expressed as percentages of average milk production, as in the following table.

Minimum percentage differences in milk production which will be significant at the 5 percent level with specified power

s	Power	n		
		10	20	40
10	75%	11.0	9.8	9.0
	90%	13.6	12.0	11.2
20	75%	7.8	6.8	6.4
	90%	9.6	8.4	7.8
40	75%	5.6	4.8	4.6
	90%	6.8	6.0	5.6

Notice that in this context, for a total number of daughters given, it is more efficient to have many bulls each with few daughters than to have few bulls each with many daughters. This is in contrast to the situation for detecting interactions. Similarly, use of highly selected bulls (provided that matching of the two groups can be achieved) will, by reduction of the variance between bulls, reduce the experimental error and give a more

powerful experiment. Again, the situation differs from that of detecting interaction. Optimum experimental design for one problem is thus incompatible with optimum design for the other problem.

Though these power calculations are valuable, there are other aspects which need to be considered. If it is taken that a new breed must have at least a 20 percent genetic superiority over a local breed to justify a large-scale replacement programme, a question requiring an answer is, what is the chance that a new breed having the required genetic superiority would fail the test and not be introduced? Suppose a preliminary test is to be carried out and if the new breed appears to be 15 percent or more superior to the local breed in this test, a more thorough comparison may be made. What is the chance that the observed difference in the test will be 5 percent or more, less than the true difference? There is also the chance that a new breed will appear 5 percent better than it actually is, or that a breed with 10 percent superiority will be further tested. In the notation used above, we want the probability that  $D - * > 5$  percent. Our assumptions give

$$\sigma_D = 20\% \sqrt{\frac{1}{4s} + \frac{15}{8sn}}$$

Thus, we require the probability that a standard normal deviate exceeds  $5\% / [(20\%) \sqrt{4/s + 60/sn}]$ . These have been calculated for the same range of designs and are shown in the following table.

Probability that a new breed will appear to be 5 percent worse (or better) than it really is

		n		
s	10	20	40	
10	0.1587	0.1160	0.0888	
20	0.0787	0.0455	0.0283	
40	0.0228	0.0084	0.0035	

From the results in this table, it would appear that a preliminary test of this kind using 40 sires, 20 from each of the local and new breeds, would have a very small chance of missing a breed which ought to be introduced or of suggesting further tests of a new breed which had only half of the required superiority.

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### **Appendix 5.3. Genetic differences required for introduction of new genotypes to be worthwhile**

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*By J.W. James  
University of New  
South Wales,  
Australia*

Exotic genotypes need to be imported only if they enable a desirable object to be attained either more cheaply or more rapidly than it can be achieved using only local genotypes. A rational decision can then be made by comparing the pattern of genetic change over time through introduction with the pattern produced by the use of local genetic resources. This raises the serious problem that since neither of the programmes to be compared is under single control, both patterns of genetic change are to a very considerable degree unpredictable. A breed replacement programme will proceed essentially by top-crossing bulls from the new breed. The rate of replacement will depend on the rate at which cows are replaced by cows with higher fractions of new genes. Faster replacement means that cows are culled after fewer lactations and so the cost of replacement will rise accordingly. On the other hand, the benefits of breed replacement are obtained earlier. A further problem is the extent of breed replacement, that is, what fraction of cow replacements are sired by foreign rather than local bulls. If this fraction is high, then the benefits are spread over larger numbers of cows than when only a small part of the population is involved in replacement. One would guess that in practice both the speed of replacement and the fraction of replacement would be greater for foreign breeds which were vastly superior to local cattle than for moderately superior breeds. Thus, in practice, it seems likely that the benefits of replacement would show a non-linear relation to differences in productivity and therefore would be much more difficult to quantify by "discounted gene-flow" methods than is an integrated programme under one direction. Similarly, in practice, we need also to evaluate progress arising from selection within the local population for comparison with progress through introduction. If selection in the local population is already efficient, there is not much difficulty, but when the local breeding programme is very inefficient, it may be necessary to obtain an assessment of likely changes in the system; both changes in efficiency and the time-scale in which such changes take place are involved.

Yet another factor requiring evaluation is the system by which foreign genotypes are tested. The larger the scale on which a new breed is tested, the greater the cost. However, the chance of making a good decision is also increased. Further, a very convincing test result may help to speed replacement. It should be noted that comparison of top-cross progeny of foreign bulls with local animals is likely to be biased in favour of the foreign bulls because of the occurrence of heterosis, which is likely to be of the order of two to five percent of productivity. This heterosis would be lost after breed replacement. Suppose a foreign breed is ten percent better than a local breed and shows five percent heterosis. Then the first progeny would show ten percent superiority (five percent breeding value, five

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*Working Paper No. 4. Prepared for the APC Expert Panel  
investigating the Introduction of New Dairy Cattle Genotypes  
into Australia. April 1975.*

percent heterosis). If heterosis were ignored, it would then be predicted that replacement would improve productivity by 20 percent rather than by the true value of ten percent. It is to avoid the problems of heterosis in genotype evaluation tests that the importation of pure-bred bulls and cows is useful, rather than in the provision of a nucleus for expansion. Expansion will be mainly by top-crossing or up-grading even when a pure-bred nucleus exists.

In view of the complexities and the parameters for which reasonable values are not available, it does not seem worthwhile to attempt a detailed analysis of the economic advantages of a breed replacement programme. However, E.P. Cunningham, in a paper presented at the Zeist Conference, considered breed replacement under the assumptions that both breed replacement and selection in the local population are carried out efficiently. He reached the conclusion that breed replacement was not "likely to be a real option unless the mean difference between the native and imported breeds exceeds 20 percent". A difference of this magnitude should not be hard to detect as significant, so if the conclusion is correct, there is no need for elaborate testing programmes, at least in the first stages, since it should be possible to estimate fairly easily which foreign strains are serious candidates for replacement of local strains. Later work may need to be more accurate, though if differences between possible replacements are small, it may not matter much which is chosen.