Developing cross-breeding structures for extensive grazing systems, utilising only indigenous animal genetic resources

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1. Introduction

Not more than a third of a century ago, a comprehensive theory of systematic cross-breeding in farm animals was fully developed (Smith, 1974; Moav, 1966; Dickerson, 1969; Dickerson, 1973). Since then many experiments have been conducted to provide information about the effect of crossing breeds or strains within farm animal species. Based on these results, efficient industry cross-breeding enterprises have been developed in poultry and pigs. In grazing species, however, even in developed countries, cross-breeding is still a matter of individual farmers who differ very much in their judgement of appropriate mating systems and breeds to be involved.

This paper presents an introductory overview of systems of breed utilisation and of the benefits that can be drawn from various mating systems. Secondly, characteristics of grazing systems, herd management and indigenous genetic resources in the tropics are briefly discussed. The last part deals with the conditions and prerequisites for the application of various cross-breeding systems for grazing livestock in the tropics when only indigenous breeds are to be used. It tries to develop guidelines which may be helpful to recognise, assess and perhaps overcome the constraints in the conditions of developing countries.

2. Systems of breed utilisation

2.1. Benefits from cross-breeding compared to pure-breeding

The major benefits from cross-breeding compared to pure-breeding can be summarised as follows:
- use of complementary breed differences;
- avoiding antagonistic genetic relationships between traits;
- use of heterosis;
- improving within breed selection response;
- adaptation of specialised breeds to different environments.

Complementary breed differences may be the most important reason for switching from pure-breeding to cross-breeding, at least in meat producing animals. Moav (1966) first discussed this effect which occurs without heterosis for single traits. He called it “sire-dam heterosis”. The efficiency of meat production is greatly increased when dams of a breed that produces offspring with less cost are mated to sires of a breed specialised in superior growth and carcass traits. In other words, the traits or trait groups in the different genotypes complement each other in their contribution to meat production. Sellier (1976) pointed out that complementary breed differences are mainly due to differences in maternal traits. In addition to differences in adaptation of dams to the environment, these differences can either arise from different performance in the number of offspring reared per dam (e.g. in sheep) or from different maintenance requirements of dams due to their body size (e.g. in cattle). Extreme examples are mating sires of the Texel or Suffolk breed to dams of Finnish Landrace or Romanov in sheep or mating Charolais bulls to Jersey cows.

Antagonistic relationships between traits are most common in animal breeding. Genetic antagonism between meat and egg production traits was the main reason for the strict differentiation between the laying hen and broiler industry in poultry. The incompatibility of stress resistance, prolificacy and meat quality on one hand with superior carcass conformation and muscling on the other is claimed to be one of the major reasons for cross-breeding in the continental pig industry of Europe. Many investigations have shown that similar antagonisms are also prevalent in grazing species. Breeds with high performance in maternal ability such as fertility and milk yield are seldom sufficient in producing carcasses of high quality. The last decades have shown that the dairy industry based on cattle moves in a direction comparable to that in poultry. Breeds which were formerly known and used as dual purpose breeds have now been transformed into single purpose breeds. Poor meat production of dairy breeds is tolerated and one tries to compensate this insufficiency by crossing beef bulls to surplus cows in the dairy herd.

Heterosis is the superiority of cross-bred animals when compared to the mean of their parents. It is expected to be proportionally related to the degree of heterozygosity. Cross-breeding increases heterozygosity whenever inbreeding has led to a higher frequency of homozygote loci than expected from Hardy/Weinberg equilibrium. More importantly, heterozygosity is increased whenever there is a difference in gene frequencies between the parental breeds. Heterosis occurs on an individual (direct) level when the performance of cross-bred offspring is compared to that of pure-bred offspring, i.e. individual heterosis is measured on F_1 animals after the first cross of two pure-breeds. Maternal heterosis is measured when dams of the F_1 generation, mated to any breed of sire, are compared to dams of the parental pure-breeds mated to the same type of sire. In other words, maternal heterosis appears after a secondary cross-bred generation such as the F_2 (*inter se* mating of F_1 animals), the back-cross to F_1 dams or three-way crosses. Less important, but commercially used in four-way crosses, there can be paternal heterosis when mating to F_1 sires leads to superiority compared to mating with pure-bred sires.

Improved selection response is expected whenever parental lines are specialised. When production is based on a pure-bred or multi-purpose population, all traits in a general breeding objective are to be improved simultaneously. In the specialised line, however, selection can be concentrated on a reduced number of traits. Thus, for example, in a terminal sire line (from which sires are used to produce cross-bred products which are all slaughtered), all traits related to female reproduction can be widely ignored. The lower the number of traits in the breeding objective, the higher is the expected selection response for single traits. Thus, the genetic response realised in cross-bred animals is increased as they get half of their genes from each of the parental lines.

Adaptation of specialised breeds to different environments is used in stratified crossing systems such as that with sheep in Great Britain. Hill breeds specialised in hardiness are kept in harsh environmental conditions on top of the stratification. “Draft ewes” of these breeds (e.g. Scottish Blackface, Swaledale or Welsh Mountain) being advanced in age are transferred to uplands to be mated to sires of Longwool breeds (Bluefaced Leicester, Border Leicester or Teeswater) to produce a first cross generation. F_1 females reared in these conditions are genetically improved for maternal traits and are transferred to intensive downland areas where they are kept as ewes to produce terminal slaughter lambs after being mated to a terminal sire line (primarily Suffolk). There are various modifications of this “standard stratification”. F_1 ewes determined for terminal crossing in lowlands can be produced directly in the hill flocks, draft pure-bred ewes are put to the lowlands (leading to two-way terminal crosses) or Suffolk rams are placed in the position of Longwool sires (leading to terminal back-crosses). A good example for stratification in subtropical conditions is the three-tiered prime lamb industry structure in Australia. Here, Merinos stand in the position of the hill breed, the F_1 ewe is a Border Leicester cross and the terminal sire is mainly Poll Dorset.

In cattle, a similar kind of stratification leading to three-way crosses is used in the British dairy and beef industry. Friesian dairy cows not required for replacement are mated to beef bulls of medium sized breeds such as Hereford. Female cross-breds are used as replacements for cows in beef herds in less intensive conditions where they may be mated to bulls of a third beef breed such as Charolais. Opposite to sheep, here the intensive environment with high-producing dairy cows is on top of the stratification and the terminal product is generated in extensive conditions.

2.2. Detrimental effect of epistatic gene recombination

Dickerson (1973) stressed the importance of recombination loss in secondary cross-bred generations. Any selection in pure-bred populations is assumed to have accumulated favourable additive epistatic gene combinations. These are partly disarranged after crossing so that the genetic source of heterosis in the F_1 generation can be considered as a mixture of (usually favourable) dominant and (unfavourable) epistatic effects. Of course general results show that advantageous dominance exceeds detrimental epistasis in the F_1 generation. Secondary cross-bred generations have a reduced expected heterozygosity so that the heterosis retained can be predicted from the relative degree of heterozygosity. However, the performance of secondary cross-bred generations predicted through the expected drop of heterosis can be substantially over-estimated when recombination loss in parental gametes is neglected. Various cross-bred generations differ in the amount of expected recombination loss. Most disadvantageous from that point of view are cross-bred generations in which both sires and dams are cross-bred animals. This holds mainly for generations such as the F_2 and composite breeds.

2.3. Mating systems

Systems of breed utilisation can be characterised according to their characteristics when considered as production systems. Production is either based on one breed only or on the utilisation of more than one breed. Production with one breed occurs either on a breed kept pure without any introgression of genes from another breed or when production is based on a composite breed. Production with more than one breed can be some form of “static” terminal crosses where the terminal product is not used for replacement. A second group of production systems with more than one breeds is that of rotational systems. In rotational systems there is no typical terminal product; females of cross-bred generations are further used for reproduction. The systems of breed utilisation are listed in Table 1.

If there is no genetic drift or inbreeding after formation of a composite breed, the heterosis retained in a synthetic is expected to be $1\text{-}Ep_i^2$ where p_i is the gene proportion of the breed i. This is true for each of the various levels, i.e. direct, maternal and paternal. Heterosis can be used most in a four-way terminal cross, a three-way cross misses paternal heterosis and in a two-way cross both maternal and paternal heterosis cannot be used. In rotational crosses the utilisation of heterosis is intermediate. Terminal crosses enable the differentiation between specialised sire and dam breeds and thus benefit from complementarity, from avoiding genetic antagonisms and from improved selection response due to specialisation. They also allow optimal breed adaptation in a stratified cross-breeding scheme but suffer from the need to replace the cross-bred females from pure-bred parents which makes self replacement difficult. This can be avoided by rotational cross-breeding which, however, can have the disadvantage of variable genotypes from generation to generation, both as dams and as finishing products. The advantages of using specialised breeds can be used in modified systems of rotation. The terminal rotation

Table 1. Systems of breed utilisation[1]

Mating system	Symbol	Heterosis Dir.	Heterosis Mat.	Heterosis Pat.	Recomb.loss Dir.	Recomb.loss Mat.	Compl.	Breed adaptation	Uniformity of products	Self replacement
Production with one population										
Pure-breeding		-	-	-	-	-	-	-	+++	Yes
Synthetics; two breeds, balanced	$(AB)_{Syn}$	1/2	1/2	1/2	½	1/2	-	-	++	Yes
Synthetics; three breeds, balanced	$(ABC)_{Syn}$	2/3	2/3	2/3	2/3	2/3	-	-	++	Yes
Terminal cross-breeding										
Two-way cross	B*A	1	-	-	-	-	+++	+++	+++	Yes [2]
Two-way cross, synthetic dam line	C*$(AB)_{Syn}$	1	1/2	-	¼	-	+++	+++	++	Yes [2]
Three-way cross	C*BA	1	1	-	¼	-	+++	+++	++	No
Four-way cross	CD*BA	1	1	1	¼	-	+++	+++	++	No
Back-cross	B*BA	1/2	1	-	¼	-	+	+	++	No
Rotational cross-breeding, controlled mating										
Two breeds; balanced	$(AB)_{Rot}$	2/3	2/3	-	2/9	2/9	-	-	-	Yes
Three breeds; balanced	$(ABC)_{Rot}$	6/7	6/7	-	2/7	2/7	-	-	-	Yes
Terminal rotation	C*$(AB)_{Rot}$	1	2/3	-	2/9	2/9	+++	+++	+	Yes
Two breeds; breed preference	$(AAB)_{Rot}$	4/7	4/7	-	2/11	2/11	-	-	-	Yes
Two breeds; generation preference	$(AB)_{Rot}$	2/3	2/3	-	2/9	2/9	+	(+)	(+)	Yes
Rotational cross-breeding, uncontrolled mating										
With dam identification		>1/2	2/3	-	2/9	2/9	-	-	-	Yes
Without dam identification		>1/2	>1/2	-	>2/9	>2/9	-	-	-	Yes

[1]The number of + symbols indicates the degree of use.
[2]Self replacement difficult in small herds/flocks.

or criss-out-cross allows mating a part of rotational dams to sires of a terminal sire breed. In a rotation with generation preference one of the breeds involved can be a specialised sire breed and the production is mainly based on dams of that generation which contends the least gene percentage of the sire breed. There are also rotations where controlled mating or breed of sire identification are not feasible.

When recombination loss is expected, this is most harmful for composite breeds. More details about the different cross-breeding systems will be discussed later in the context of their application to grazing livestock in developing countries.

3. Grazing systems and herd management

3.1. Grazing systems

Grazing of animals occurs in various conditions, ranging from some form of roadside grazing in small units to large-scale ranch management systems. In this paper extensive grazing systems will be considered under the aspect of access to controlled mating which is a prerequisite for the realisation of systematic cross-breeding. One criterion of access to controlled mating is herd / flock size and management and thus the grazing systems will be classified into four categories as shown in Table 2 (Williams, 1981).

Table 2. Grazing systems and constraints to controlled mating and identification (CM/I).

System of grazing	Area of predominance	Access to CM / I[1]
Nomadic	Developing countries (DC)	(+)
Semi-sedentary	DC	(+)
Transhumance	DC and temperate countries	++
Sedentary		
• Smallholder	DC	+++
• Village herds	DC	(+)
• Ranching	DC and temperate countries	+++

[1]The number of + symbols indicates the degree of access.

According to the evolution of the relationships between man and grazing species, the ***true nomadic system*** may be mentioned first. It is becoming more and more uncommon for a variety of reasons. Nomadic tribal groups operating in this system do not have a built home base. Herds, flocks and people move within a tribal territory following the rains to areas with sufficient plant growth. Usually the herd in the system contains a mixture of various species, predominantly cattle, sheep and goats.

Second, s***emi-sedentary systems*** are based on a built village permanently occupied by the women and children. The herds are absent for extended periods and usually attended by men and boys such as in the Maasai tribe of eastern Africa.

Transhumance systems are applied in developing as well as in developed countries. They differ from semi-sedentary systems in that the trek is cyclical. In Mediterranean countries, for example, it begins at the end of winter with the flocks and herds moving to the mountain pastures. The shepherds or herders bring the animals back to the lowlands at the end of summer.

As a last group of systems in this classification, the ***sedentary systems*** include the majority of the world's livestock. There are three basic types with a variety of modifications. First there is the smallholder section. Ruminants are kept in a low external input system, fed partly on a mixture of crop residues and more or less extensive grazing. A rather old and traditional system concerns village herds or flocks herded on surrounding common or private lands and taken into yards, corrals, folds or byres during the night. The last one took its rise as a consequence of developing industries in the last two centuries. This is the open range or ranching system, originally developed in North America, Australia, New Zealand and parts of South America. This system still has a growing tendency. It is characterised through sub-divisional fencing, provision of water and with very few exceptions, no housing in winter. Buildings are limited to shearing and machinery sheds as well as animal handling facilities such as yards and dips.

Typical grasslands with extensive grazing are steppes, veld (South Africa), pampas (South America), plains and prairies (Northern America, Australia). These are the areas where nomadism, semi-sedentary systems and ranching predominate. Transhumance occurs in areas with diversified altitudes such as river valleys and hills at near distances. In addition to nomadism and semi-sedentary systems, smallholder units and village herds prevail in developing countries. For all systems except ranching, there is generally low capital input and a medium to high labour input; ranching is usually high in technology and low in labour inputs but has heavy capital requirements. The division of the grassland into paddocks through fencing allows for the splitting of herds into various groups.

3.2. Constraints to controlled mating and identification

Admission to controlled mating and / or identification (CM / I) in a grazing system is most important for an appraisal of the possibilities to apply systematic cross-breeding in grazing ruminants (Table 2). At a first glance, fencing in the ranch management seems to be the main reason why controlled mating and identification are widely limited to this system. This, however, should not be so. Within the transhumance system, there are examples of intense breeding activities. Sheep and goat flocks in Switzerland and other alpine countries are kept in transhumance conditions. After being shepherded in large flocks for summer grazing in the mountains, the flocks are subdivided into small groups and confined in farmers´ sheds for the rest of the year. During that time, most of the mating and lambing occurs and thus such a system is very accessible to controlled mating, lamb identification and even recording.

CM/I should not be a problem in smallholder units, both with and without artificial inseminations. For nomadic, semi-sedentary and village herds/flocks, however, the practicability of CM/I depends primarily on the qualification of personnel and its motivation to do so. In many cases personnel qualification concerning the familiarity with individual animals in the herd/flock is extremely good. At least dam identification of new-born animals can be ensured by some sort of eartagging. Sire identification is much more difficult due to natural mating with more than one sire in the herd. It is not impossible, however, to manage controlled mating through some sort of periodic sire rotation. As in most circumstances, sires cannot be separated from the herd/flock, the use of harnesses for mate prevention could be arranged so that in a certain period the new-born offspring can be identified for paternal ancestry.

4. Characteristics of indigenous genetic resources

4.1. What are indigenous breeds?

A definition of what we refer to as indigenous breeds seems to be necessary. Criollo cattle in South America and Merino sheep in many semi-arid regions in the world have a pure European origin. Santa Gertrudis cattle and Dorper sheep have at least one half of their genes from indigenous non-European breeds and have lived in the tropics since the first decades of the 20th century. What is indigenous? In this paper, new breeds formed in the 20th century which have genes from improved temperate breeds from Europe or North America are referred to as non-indigenous. This includes e.g. Santa Gertrudis, Charbray and Droughtmaster cattle as well as Dorper sheep. Breeds or strains from Mediterranean countries will be considered non-temperate. Since both Criollos and Merinos originated from the Iberian peninsula and were also introduced in non-temperate countries long before the 20th century, there is no doubt we consider them as local breeds. So far the distinction is straightforward. A question arises concerning modern breeds selected in Mediterranean conditions and introduced and crossed in tropical countries, such as the fertile Chios sheep from Greece or the Lacaune dairy sheep from the south of France. Let us call them indigenous with a question mark.

In contrast to most countries in temperate zones, genetic resources in tropical livestock can rarely be considered as consolidated breeds with a certain uniformity and a common breeding goal. Only a few of these populations are managed genetically by a breed society that maintains a stud book and performance records. Symptomatically, breed names in many areas vary substantially and are quite often rather artificial. Reports from livestock populations in India are most honest when talking about "non-descript" breeds. As a result, unusually high levels of phenotypic variations can be observed in these populations which led Timon (1993) to the suspicion that major genes with significant effects on production traits may be segregating in these populations. Here a rough characterisation of breed groups is presented according to their suitability for utilisation in cross-breeding. Furthermore, a brief description of the few outstanding breeds which have systematically been selected will be given.

4.2. Breed groups in cattle

Many *Bos taurus* and all *Bos indicus* cattle strains can be characterised as indigenous breeds with a long history of adaptation to tropical conditions (Table 3). For many centuries, taurine breeds have settled in Western Africa and widely adapted to trypanosomosis in the tse-tse fly areas. In the humid climate the size of these breeds remained small. An outstanding breed due to its trypanotolerance is the N'Dama breed. Since the 16th century, European settlers brought cattle from the Iberian Peninsula to Latin America which were then called Criollos. They have been adapted to tropical and subtropical conditions, but due to the overwhelming imports of European and improved Zebu breeds there was nearly no organized selection of any breed. Taurindicus strains (Sanga) were kept by African tribes, mostly in East and South Africa, long before the new composite breeds between *Bos taurus* and *Bos indicus* were formed in the 20th century. The most well-known breed selected for beef (originally draught) is the Africander breed of South Africa. More recently, breeds from Zimbabwe and Botswana such as the Tuli, have received attention because of their beef performance.

Bos indicus cattle were brought to Africa many centuries ago and also to South and North America since the 19th century. In southern states of the USA, the Brahman breed has been selected as a beef breed for tropical conditions. Zebus in India are of miscellaneous size and quality due to its multipurpose use for draught, milk and manure. Zebus in Africa are mostly of small size except the Boran which has been developed for beef by a breed society in East Africa. Zebu beef breeds have also been selected by breeders in Latin America who formed breeds such as Nellore and Indo-Brazil. Less efforts have been devoted to developing dairy strains from the Zebu gene pool, e.g. from Sahiwal and Red Sindhi.

4.3. Breed groups in sheep and goats

As cattle, sheep and goat populations in the tropics should be considered from the viewpoint of their suitability for milk and meat production. Wool, pelt and skin may either be considered as by-products of dual purpose breeds or if specialised in a specific market, confined to special pure-bred populations such as Merino strains or Karakul in sheep and Angora or Cashmere strains in goats. In both species there are a variety of populations which differ in many aspects. Size and weight are considered to be most important as they are the major criteria concerning the suitability for meat and to a lesser extent, also for milk production.

Mason (1991) classified sheep breeds according to fleece and tail type. There are a variety of large, medium and small-sized breeds either

Table 3. Classification of indigenous breed groups in ruminant species.

Species and groups	Main characteristics	Superior breeds
Cattle		
• West African taurine breeds	Trypanotolerant, small	N'Dama
• Latin American taurine breeds (Criollos)	Miscellaneous sizes	-
• African taurindicus (Sanga) breeds	East and South Africa	Africander, Tuli
• Small Zebu breeds	e.g. East Africa	-
• Large Zebu breeds	India, Africa, America	Brahman, Boran, Nellore Sahiwal, Red Sindhi
Sheep		
- Large sheep breeds	Mainly wool sheep	Somali, Awassi, Chios?, Lacaune?
- Small sheep breeds	Hair and wool sheep	-
- Prolific sheep in the tropics	Polygenic inheritance	D'man, Barbados Blackbelly
	Major gene responsible	Booroola, Javanese Thin-tail
Goats		
1) Large goat breeds	Arid or semi-arid areas	Boer, Damascus, Jamnapari
2) Small goat breeds	Humid areas	-

short-tailed, thin-tailed, fat-tailed and fat-rumped within both fleeced and hair sheep breeds. Furthermore, there are breeds with outstanding prolificacy such as the Booroola Merino from Australia (Piper *et al.*, 1985), the D'man from Morocco (Lahlou-Kassi and Marie, 1985), the Javanese Thin-tailed breed from Indonesia (Bradford et al., 1986) and the Barbados Blackbelly hair sheep from the Caribbean (Rastogi, 1996). The prolific breeds Han and Hu have been reported from China (Feng et al., 1996) from which particularly Hu seems to be well adapted to subtropical conditions (Notter, 1996). Irrespective of whether there is polygenic inheritance of the trait or whether a single gene is responsible, these breeds provide potential indigenous resources for improving the maternal potential of native breeds in improved tropical conditions. DNA technology will facilitate the introgression of major high-fecundity genes.

An outstanding large breed of sheep for meat production has been developed on the basis of the black-headed Somali hair sheep in South Africa. The breeding society calls it Blackhead Persian and a derivation from this is also bred in Latin America under the name Brazilian Somali. Part of the widespread Awassi sheep in the Near East has been selected efficiently as a superior dairy breed. As already mentioned, dairy breeds developed in Mediterranean conditions may be suitable when the aim is to improve milk production from sheep in developing countries. While some information about crossing Chios with breeds in the Middle East (Aboul-Naga, 1996; Notter et al., 1996) exists, the suitability of the intensively selected French Lacaune breed for subtropical conditions has still to be proved.

Domestic goat breeds in tropical countries vary considerably in size and body weight. A speciality of goat breeds is that dwarfism has not revealed to be a handicap for goat husbandry in many conditions. Particularly in Africa where goats are primarily used for meat production and seldom milked, there are many extremely small breeds. Like in cattle, it is the small breeds which are kept in tse-tse-fly infested areas and thus have developed trypanotolerance. On the other hand, there are a few large breeds specialised in milk or meat. In minor improved husbandry conditions, indigenous dairy goat breeds can hardly compete with cross-breds that are improved by introgression of genes from European breeds. However, native dairy breeds with some superiority, e.g. the Damascus goat from the Middle East and the Jamnapari from India, may be important in less favourable conditions. An exceptional local breed systematically selected for meat production is the Boer goat from South Africa.

5. Suitability of various cross-breeding systems

The intention of a synthesising / upgrading programme is to create a new breed by introducing genes of a foreign indigenous breed. Various prerequisites are required when this is to be established and are described as follows.

5.1. Composite breed formation and upgrading

a. The programme should be a cooperative enterprise.
Based on animals of a local breed, a new breed is to be created. That means, in the long run any mating and selection will be realised within this new population. The population to be changed should not be too small. It is obvious that with an increasing population size the risk of inbreeding depression declines and the probability of genetic improvement through selection increases. In other words, before starting the programme, there should be a certain probability that enough farmers / stockholders are willing to join the scheme.

b. There is an agreement about the concept of a new breed.
The members of the cooperative agree that selection within their own breed takes an unacceptable long time compared to the progress that can be obtained through introduction of genes of another breed. There is also an agreement about the foreign breed from which genetic material should be introduced. Although there are usually no figures about the real superiority of the foreign breed, they have a common idea of the genetic constitution of the new breed, but do not know what the optimal proportion of foreign genes should be.

c. There is a central organization of the process.
The introgression of foreign genetic material is to be managed efficiently. Most reasonable seems to be the creation of a central station for sires that carry the genes of the desired foreign breed. If artificial insemination is possible, there can be a central deposition of semen doses. The station can be run by a state farm, a cooperative or a private unit. A minimum of educated technical personnel is required to manage the service of the station, supply the clients with the genetic material, collect and analyse some data and to take care of mutual information between the station and the participants.

d. Sires of the foreign breed should be carefully selected.
In contrast to the introduction of genetic material from temperate breeds in developed countries, knowledge about characteristics of another indigenous breed is usually scarce. With few exceptions, these breeds are not genetically structured as temperate breeds and there are normally no breeding values of single males. It is expected that phenotypic variance in these breeds is very high which complicates the assessment of the genetic merit of individual animals. Furthermore, there are usually insufficient records about measures of disease control in these breeds and the danger of introducing infectious diseases is quite high. In a first step, the number of sires selected should not be lower than between five and ten. For several reasons, an introduction of embryos or females of the foreign breed is considered not to be cost-effective.

e. First crosses are accompanied by the installation of an information system.

In a first step, pure-bred sires of the foreign breed are mated to dams of the local breed in order to produce F_1 animals. This first step of gene introduction is to be accompanied by a minimum of recording and information. Initial information should be collected about survival, growth and other characters of interest in the growing F_1 animals. Sire identification is to be insured for both the farmer and the staff of the central station. After a first round of cross-bred matings, a meeting should be arranged where preliminary results and experiences are exchanged.

f. The central station takes care of providing sires to mate F_1 females.

From the first batch of F_1 cross-breds, young males are selected by the station personnel and bought or rented for rearing in the station. To avoid risk of inbreeding and genetic drift, rearing of about two sons per sire is recommended. If the first meeting has demonstrated a positive reaction, about one half of the F_1 females are mated by F_1 sires to produce animals of an F_2 generation. Another half is back-crossed to pure-bred sires of the foreign breed. The mating of sires with their half-sibs (in case of F_1 *inter se* matings) or with their daughters (in case of back-crosses) are to be prevented. As in the F_1 generation, a sire identification of new-born F_2 and back-cross animals is to be insured. F_1xF_1 and back-cross matings are followed by collection of information and data about the maternal performance of F_1 dams (e.g. dystocia, fertility, suckling or milk performance) and juvenile traits of their offspring (e.g. survival and growth). After a second meeting with exchange of this information, first decisions about the further choice of sires will be made.

g. A further strategy based on F_2 and back-cross information is organized.

After rearing F_2 and back-cross animals and first assessments of maternal characteristics, the results of a third meeting and the conclusions to be drawn may be as follows:

Results	Conclusions
• All cross-breds are inferior to pure-breds	• Further matings with sires of the local breed and the upgrading scheme are abandoned
• F_2 generation is better than back-crosses	• The station keeps and produces F_1 sires for further matings; a part of cross-bred females are mated to local sires
• Back-crosses are superior to the F_2 generation	• The station rears back-cross sires for further mating and tests a next step of back-crossing to the foreign breed

In the second case (F_2 superior to back-crosses) it should be checked whether a lower gene percentage of the foreign breed would have been enough. Therefore, a part of the F_1 and F_2 animals is back-crossed to pure-bred sires of the local breed. If the F_2 maintains its superiority, a continuous selection and supply of F_1 sires as proposed by Cunningham and Syrstad (1987) should be organized by the central station. F_1 sires are produced by a steady selection of sires or semen from the foreign breed and by mating them to the best cows of the F_2, F_3 and further generations. This ensures that inbreeding will be minimised and if there is an efficient selection programme in the foreign breed, guarantees that the new population benefits from the continuous genetic improvement in this breed. In Case 3 (back-crosses superior to F_2) the same benefits can be drawn from a continuous supply of selected sires of the foreign breed.

h. The station initiates a recording and selection scheme.

Any new breed formation or upgrading is useless if prerequisites of further selection are not available. A by-product of the upgrading scheme was the initiation of an information system and the introduction of common decision-making. Data and observations were collected and analysed and meetings were organized. During this process it is quite likely that some of the participating farmers have shown to be most interested and active. They should be stimulated to continue their activity and form the nucleus for further breeding policy. They should be the basis for a continuous and slowly extended recording scheme. The staff of the station are responsible for data collection and will be educated in computerised estimation of breeding values. Regulations for a further breeding strategy and the creation of a breeding society should be negotiated and realised.

5.2 Terminal two-way crossing

In contrast to cross-breeding for new breed formation, terminal crosses of two pure-breeds can usually be managed on a single farm level. Motivation, conditions and prerequisites for changing from producing with pure-bred animals to single two-way crosses may be the following.

a. The farmer is interested in improving meat performance.

Except in egg production where the terminal product is the laying hen, terminal two-way crosses are particularly important for meat producing systems with farm animals. Dams of a breed sufficient for maternal traits are mated to sires of a specialised meat breed with superior growth and carcass performance. In nearly all production and marketing systems with ruminants, the farmer can profit from animals with genetically improved meat performance. Exceptions may be very specialised systems of pelt or fibre production in extreme conditions (e.g. Karakul pelts, mohair or cashmere wool) or dairy production with cattle in most parts of India where beef is not consumed.

b. The environment allows the exploitation of genetically improved meat performance.

Very often the dams of the local breed are best adapted to the harsh conditions of the farm and the farmer is willing to continue keeping these dams. For the surplus offspring determined for slaughter, however, feed and husbandry conditions can be provided which are sufficient for animals with a potential for meat production higher than that needed for pure-bred offspring of the local breed.

c. There are indigenous breeds with a higher potential for meat production.

In many tropical conditions the adaptation process was accompanied by a reduction of body size and weight. Examples may be Criollo strains in high altitudes of Latin America or small Zebu strains in Africa which, over the centuries, ended up with smaller body sizes than their ancestries of the Iberian peninsula or of India. Furthermore, adaptation also seems to occur with a reduction of fleshiness, meat proportion and conformation. There is no doubt that for many small and "bony" breeds in the tropics, there are indigenous breeds with a higher meat performance. Examples have been mentioned in Chapter 4.

d. There is continuous availability of sires from superior meat breeds.

One of the reasons for the poor application of two-way cross-breeding may be that there is no steady, uniform and cheap supply of sires from superior meat breeds. A prerequisite for continuity and uniformity would be a genetically structured breed of that type. The structure should guarantee the existence of a nucleus level of breeders who are ready to supply sires with reliable quality, uniformity and price. Furthermore, the distance to the breeder should not be too far due to transport costs. It should be mentioned that the use of semen instead of sires for natural service seems highly impracticable in present conditions of developing countries. This is particularly true in our case where both the recipient of semen doses (the one who crosses) and the donator (the breeder of the indigenous sire breed) should have access to an AI service which is hardly thinkable. Even in a large dairy herd applying AI, the meat sire may be preferred to be used in a "clean-up" natural service instead of as a semen dose.

e. The sires of the meat breed can be kept cheaply and in good breeding conditions.

Keeping sires of a second breed depends on the size of the farm and on facilities to guarantee an appropriate environment for maintaining its breeding conditions. A large cattle herd or sheep flock always uses more than one sire. For a sustained breeding condition and long productive lifetime it may be sufficient to separate it from time to time and feed it in improved conditions. Small herds / flocks may keep either one or, in most cases, no sire at all. They rely on a village, communal or private sire station. Under these circumstances it should be easy to keep sires of more than one breed. A prerequisite for a cheap supply is that the small farmer shares the sire with other farmers.

f. The use of a second sire breed does not impair a continuous female replacement.

Self-replacement of females is essential for the majority of livestock owners in developing countries. This is particularly true for smallholders with a high degree of self-sufficiency where the loss of a cow, ewe or doe means a substantial jeopardy of the family's welfare and security. If the smallholder is not willing or unable (e.g. due to lack of cash) to buy replacement dams, there is almost no chance of using two-way terminal crossing. In small herds or flocks the risk of an insufficient own dam replacement is tremendous. If, for example, the average cow gives birth to four calves during her lifetime, a farmer not willing to buy missing replacements should have a herd size higher than about 15 cows (Gerhardy, 1986). If he has a very large number of dams, or if he is prepared to buy any missing own replacement, the maximal capacity for terminal crossing is 1-2 / n, where n is the average number of live offspring reared per dam and suitable for breeding. For n=2, 3, 4, 5 or 6 this means a proportion of 0, 33, 50, 60 or 67 percent of cross-bred matings.

g. Controlled mating and individual identification are useful.

An optimal procedure would be to take the genetically best females for replacement through pure-bred matings and cross the rest to sires of the meat breed. If dystocia from mating meat sires is a problem, young dams should be used for replacement and the older ones can be crossed. For both of these targets, controlled mating would be required. Where this is not feasible, at least breed of sire identification for new-born offspring were useful, e.g. through using harnesses (marking mated dams, periodic exchange of breed of sire) or simple genetic colour marking of the two genotypes.

h. The reproductive performance should not be too low for extra cross-bred matings.

There may be specific situations where the number of offspring reared and suitable for replacement is not higher than the number of replacements required. This means that n (in paragraph f) is near 2.

Heterosis is not essential for the efficiency of terminal two-way crosses to improve meat production. The main reason for its use is the sire-dam complementation. In most conditions with tropical breeds and environments, the reason for complementarity will be breed differences in size rather than in reproduction performance. Mating dams of a small breed with low maintenance requirement to sires of a large breed means that the proportion of feed directed to growing animals is increased. Of course, the size of the dam breed should not be too small for dystocia to be a problem.

Any interest in terminal cross-breeding will depend on the socio-economic constraints that keep the farmer away from a more market-oriented animal husbandry. So far the majority of livestock in developing countries is kept as multipurpose animals. They have to provide the farmer or family first with milk and meat and secondly, with draught power, manure, fibres, hides and skin. Farms with any market-oriented specialisation are rare. As long as a certain degree of specialisation with stock exchange between farms is not reached, any interest in terminal crossing will be poor.

A first stimulation for cross-breeding could arise if some farms specialise in fattening meat animals or if there are organizations interested in establishing some kind of feedlots. These should find other farmers who are prepared to renounce keeping their surplus offspring up to slaughter age and who can expand the number of dams instead. Feed and husbandry conditions in the fattening units will be managed differently from those in the farms which keep the dams so that the issue mentioned in paragraph b) will be accomplished. A second but more unrealistic encouragement to use cross-breeding could arise if stratification of production is further expanded so that not only fattening and dam-offspring enterprises are separated in different units, but also the dams are replaced at different locations. Under these circumstances, the concern discussed in paragraph f will not be a problem.

A brief look at the situation in more advanced livestock industries in developed countries may be helpful to assess the chance of more terminal cross-breeding in tropical conditions. Sometimes the issue c) (no better meat breed available) may not be true in a herd or flock. This is only possible if the animals belong to a breed that has all characters of a typical terminal sire breed. However, meat production with this breed can hardly be competitive as genetic antagonisms will prevent the breed from having satisfactory maternal characteristics. A farmer with such a type of animal will therefore try to sell sires which are used for terminal crossing in another breed. In other words, he will be a breeder within a cross-breeding system rather than running a typical commercial herd or flock. Another example without terminal crossing is the majority of dairy farms in temperate livestock enterprises. Dairy farming is mainly based on pure-bred cows that are extremely specialised in milk and quite insufficient in growth and carcass traits. That means, the issue in paragraph c) is more than realised. However, the average number of lactations in e.g. Holstein herds is usually lower than three. Under these circumstances it is paragraph g) which is responsible for producing with pure-bred cows without any terminal crossing.

5.3. Stratified terminal cross-breeding

Advanced production systems for white meat species (e.g. pigs and poultry) are mainly based on terminal crossing using F_1 dams. The pig and poultry industries are hierarchically stratified. Multipliers cross parental pure-breds to produce F_1 replacement females for commercial units where the terminal slaughter products are reared and transferred to commercial finishing units. A terminal sire is mated to the F_1 females to exploit complementarity and direct heterosis in addition to maternal heterosis in the dam. Sometimes the terminal sire itself is a cross-bred animal contributing paternal heterosis. The number of breeding animals in the pure-bred parental lines involved in the system is very low. The genetic improvement of these lines lies in the hands of internationally operating companies. The lines are selected differently according to their specific position in the cross-breeding system.

Although the livestock industry of grazing animals in developed countries is also highly specialised and market-oriented, there are no organized cross-breeding strategies in ruminants similar to those in pigs and poultry. The reason is not that genetic effects used in cross-bred animals such as heterosis and complementarity were smaller (Nitter, 1978; Gregory and Cundiff, 1980), but simply the much lower reproductive performance of ruminants. To maintain a cross-breeding system based on F_1 dams, the number of pure-bred animals should be very large. As specialised lines by definition have a lower overall performance, their inferiority would more than offset the benefits from hybrid F_1 dams.

If a cross-breeding system based on F_1 dams should work in grazing species, the participating pure-breeds should *per se* be specialised and should be self-contained independently from a special task in a cross-breeding scheme. Specialisation of breeds has always occurred when they had to adapt to special environmental or production conditions. Examples of specialised breeds and their use in stratified cross-breeding systems have been mentioned previously (see Chapter 2.1). We will show various conditions and prerequisites for the realisation of stratified crossing and discuss it with regard to conditions in developing countries. These are the following:

a. There is a market with both a demand and an offer of female breeding stock.

Production with and replacement of F_1 dams in one farm or unit is considered to be impossible as three different genotypes of dams should be kept simultaneously and under complete controlled mating. Therefore, more than in a terminal two-way crossing, certain stockholders should be willing and able to buy their female replacements from outside (recipient units). On the other hand, there should be herds or flocks which are specialised in selling replacement females (donor units).

b. Recipient and donor units have different environments.

Theoretically, in a unique environment there is only one optimal genotype of dam. Due to maternal heterosis this is most likely an F_1 dam. To produce this animal, however, a high amount of pure-bred females is required. These are expected to be worse than F_1 dams and thus are an unjustifiable burden for the system. This burden disappears if donor units produce in a different environment where a genotype different from the F_1 is adapted. Most likely this would be a harsh environment with an adapted hardy breed, whereas F_1 dams are kept in better conditions.

c. The donor unit separates or sells surplus dams for cross-bred matings.
For various reasons, the stockholder in harsh conditions may hardly be able to separate the herd or flock into two mating groups, i.e. one for pure-bred replacements and one for the generation of F_1 dams. It may be convenient for him, however, to focus on keeping as young dams as possible and transfer older and more vulnerable dams to a "sub-unit" with less hard conditions. Younger dams are expected to cope much better with the harsh environment, whereas older dams can survive and reproduce for another two or three years in the better conditions of the sub-unit. This is operated as a multiplier unit as the dams there will be exclusively mated to sires of a second breed to produce F_1 dams.

d. A specially selected sire breed is used in the multiplier unit.
Whereas the breed on top of the stratification is fixed due to its adaptation, the sire breed used in the multiplier unit should be carefully chosen. It is expected to transmit genetic improvement according to the special demands of the recipient unit. These may predominantly be maternal traits such as fertility, prolificacy and milk yield. In sheep, for example, the high fertility breeds mentioned earlier (Chapter 4.3) may be most interesting.

e. The dams in the recipient unit are exclusively mated to terminal sires.
As the recipient unit renounces own replacement, its mating strategy is most easy. Sires of a meat breed are purchased which improve growth and carcass traits according to the market demands and as far as feeding and husbandry conditions allow its genetic exploitation. All offspring born are destined for slaughter.

f. Continuous organizational activities of the recipient unit are most important.
Contracts of participants in a cooperative scheme can highly facilitate its conduct. A focal position in the scheme has the recipient unit. It knows the market requirement and its own environmental constraints. It is thus best informed about the optimal genetic qualities of the terminal sire and also of the sire to be used in the multiplier unit. Furthermore, it is most sensitive to the discontinuous supply of healthy replacement ewes with high genetic merit. Thus, it is evident that it is the recipient unit which is expected to take responsibilities and activities in the operational course of the scheme. It will be well recommended

to make contracts with owners of donor units or, if possible, run a multiplier unit on its own.

The scenario of a three-tier stratified cross-breeding system as outlined above is very similar to the stratification in the British sheep industry. As in two-way terminal crossing, heterosis is no prerequisite for the application of such a scheme. In contrast to stratified systems in pigs and poultry, there is no centrally organized operation of the system. As if supervised and managed by an “invisible hand”, the cooperation of the participants in the various tiers of the British sheep industry has been operating for two centuries. One of the reasons for its success may be the simplicity of the mating policy within flocks. In the hill breeds, i.e. on top of the stratification, there are only pure-bred matings for own replacements. The multiplier upland flocks as well as the commercial F_1 down flocks are both “flying flocks”; that means, all replacements are generated from outside and all ewes are exclusively mated to one breed of sire. In none of the tiers, except in flocks of seedstock producers, is controlled mating required to run the system. Another advantage of the system is the higher price that a hill farmer gets for a draft ewe sold for further use than for a ewe culled for slaughter. So far transformation of the system to the livestock industry in tropical or subtropical countries sounds reasonable and easy.

The most severe obstacle to the encouragement of such a system in developing countries is most certainly the high degree of specialisation required. The breeds involved in the system are no more the typical multipurpose animals that have so far been a guarantee for economic security and for avoiding risks. Instead, at least the breeds producing the sires used in the second (multipliers) and in the third stage (F_1 dam units) will be more and more specialised for their tasks in the system. Thus, a specialisation in a framework of collaborating farmers will be inevitable. The necessity of collaboration is still a barrier hard to be passed, even in the advanced livestock industry of developed countries and it is hard to believe that the establishment of a stratified cross-breeding system in conditions of the developing world will be easier.

How could we imagine a source from where cooperative stratified animal production could commence? It is easy to believe that an impulse can come from increased urbanisation with growing prosperity of the urban population. This induces demands for animal products such as meat with continuous supply and quality standards. This would stimulate livestock enterprises around the cities to specialise in satisfying the growing demands. Depending on the price relationship between meat and feed concentrates, it may be economical to intensify feeding and husbandry conditions. The shorter the distance to a city, the more interesting it is to specialise in producing the terminal products and leaving reproduction and replacement of females to more distant units with less intensive conditions. If the price / cost ratio becomes more favourable, there may be capital investment in the livestock industry and some livestock enterprises may expand to a size which allows them to control and manipulate the genetic material to be selected and used for the generation of both the end products and their mothers.

So far the discussion has circulated around the classical three-way cross within a stratified system of production. A second option, the use of a cross-bred instead of a pure-bred sire in the terminal position (four-way crosses) seems to be of pure academic interest as it may be hard enough to find at least one indigenous breed which is superior in meat production and fulfils the conditions d) in Chapter 5.2 (continuous availability of sires). More interesting is the option that the sires used in the second and third stage of the system come from the same breed. This would turn out to be a stratified back-crossing. In regions with small adapted breeds, a large indigenous breed may be found which is better in both, maternal traits and meat characteristics but lacks some hardiness. A pure-bred dam of this breed may be less economical than using an F_1 female which gets half of its genes from this breed and the other half from a small and hardy breed. In addition to heterosis and an increase in hardiness, the use of such a cross-bred female benefits from reduced maintenance requirement. A third option may be a two-tier stratification. On top there are still stockholders who like to sell surplus dams with an older age for further production in a better environment. This environment, however, can be one of the herds or flocks keeping dams of the terminal produce. The surplus dams are transferred there and directly mated to terminal sires; in this case we deal with a two-way cross.

In all options so far discussed, an adapted hardy breed is assumed to stand on top of the stratification. More than a terminal two-way crossing, stratified terminal cross-breeding thus enables low producing but well adapted breeds to play an important role in the domestic livestock industry. Otherwise endangered breeds can thus be prevented from extinction and contribute to strategies for sustainable development of animal agriculture in developing countries.

A stratification where a dairy cattle herd could be involved seems to be far from reality in a developing country. We should, however, stick to the discussion of opportunities to use stratified crossing for meat production in ruminants. Which grazing system could be most suitable to take part in such a system? Extensive grazing systems in the tropics such as nomadism, transhumance, village herds or ranching, suffer frequently from periods with low feed supply due to drought. An important strategy to cope with drought in these conditions is to keep the stock size variable. In periods with low feed supply surplus females are sold in order to save the rest of the flock or herd. These will most likely be older dams. This means that traditional extensive grazing systems seem to be predetermined for the top position in a stratified cross-breeding system. Let us assume that there are potential multiplier units which are ready to take these surplus dams to produce F_1 dams. These, however, are forced to guarantee a continuous supply of F_1 replacements for the third tier. In other words, the multiplier stock of dams should be stable in size and not dependent on an insecure supply of surplus dams from its potential donors. The erratic availability of surplus indigenous animals may thus be a crucial point in the system. Use of extensive grazing areas with adapted indigenous breeds in the tropics and simultaneously, a continuous culling policy in the herd or flock seem to be unsurpassable contrasts for which we hardly find solutions.

5.4. Rotational cross-breeding

In contrast to static terminal cross-breeding schemes, systematic rotational crossing is much less widespread. A critical look at claimed applications of rotational cross-breeding quite often may turn out to be conducted by stockholders who change their mind about the best breed from time to time. Much more than in a two-way cross, systematic rotation is appropriate when there is a need or desire that replacements should be generated in the own herd or flock. However, as they are produced by cross-bred dams instead of pure-breds, maternal heterosis is used in addition to direct heterosis. In species with a low reproduction performance such as ruminants, a continuous replacement of cross-bred dams from cross-breds themselves seems to be most useful. This avoids the need to keep a large number of pure-bred dams for the replacement of cross-bred dams as has been the case in systems based on F_1 females. On the other hand, conventional “balanced” systems as described in most textbooks, do not allow the use of complementarity. The breeds or lines involved should not be specialised like those for terminal systems since animals are expected to be suited for both, to be good mothers or milkers and to produce good offspring for growth and carcass production. On the other hand, these requirements together with the need of no large variation between the rotational cross-bred generations, are longing for breeds which are not so different from each other. This, however, leads to the dilemma that heterosis, the original cause for rotation, may not be as high as it could be when crossing breeds with large differences in their gene frequencies. It is no wonder that conventional systems of rotation have never reached a large distribution.

A first useful alternative for conventional balanced rotation is to use rotational cross-breds as dams and mate those not needed for female replacement to sires of a terminal meat breed. This terminal rotation allows to fully exploit complementarity and direct heterosis and the final produce differs much less from generation to generation. To some degree, a similar effect can also be obtained when two breeds with some specialisation as sire and dam breeds are rotated, but different cross-bred dam generations are kept in unequal numbers, i.e. they are not “balanced”. The cross-bred generation with a higher gene proportion of the foundation sire breed is kept in a small number of dams, just the size required to sustain the replacement of the other generation. Then the majority of females in the herd or flock are those with the higher gene proportion of the foundation dam breed. This also means that most of the offspring destined for slaughter are those with a higher gene proportion of the foundation sire line. In other words, such an approach uses complementarity to some extent. Let us call this "rotation with generation preference". A third modification of conventional rotation may be called "rotation with breed preference". This is an unequal use of sire breeds in a regular sequence allowing for increased expression of additive effects of one breed (the one with the best overall performance) at the expense of reduced utilisation of heterosis (Bennett, 1987a).

So far, all options of rotational cross-breeding cause tremendous management problems in extensive grazing systems of livestock. These are the identification of individual dam' sire-breed pedigree and due to overlapping generations in the herd or flock, controlled mating through the concurrent use of more than one sire breed. Controlled mating, i.e. the mating of a defined cross-bred dam group to sires of a specific breed, may be the major constraint. Management inputs are much less when only one sire breed is used during a certain mating period ignoring the different sire-breed pedigrees of dams from overlapping generations. Let us assume that this is possible. A slight relaxation of management input may then be a dam identification for its sire-breed, e.g. by simple ear-marking. Only those female offspring are then kept for replacement which belong to the "correct matings". In an $(AB)_{Rot}$ criss-cross, for example, after mating sires of breed A only female offspring from ($^1/_3$A $^2/_3$B) dams will be identified and kept for replacement and all offspring from ($^2/_3$A $^1/_3$B) dams will be slaughtered. Let us call this "uncontrolled mating with dam identification". In these circumstances, the same amount of maternal heterosis can be maintained as in a regular two-breed rotation with controlled mating. A rotational system with the least management input is one that uses only one sire breed per mating period and without dam identification. Such an "uncontrolled mating without dam identification" was called "sire-breed rotation" by Bennett (1987b). He showed that, depending on the number of consecutive mating periods a sire breed is used and on age structure of females, an amount of heterosis higher than in a composite breed with equal gene proportions could be maintained.

The feasibility of controlled mating and dam identification in various grazing systems has already been discussed (see Chapter 3.2). As in the other systems of cross-breeding, we will step by step consider the conditions and prerequisites for the realisation of rotational cross-breeding in developing countries.

a. **Direct and maternal heterosis can be used by crossing indigenous breeds.**
   Information about heterosis for cross-breds where indigenous breeds are involved, is almost exclusively limited to crosses of indigenous with modern temperate breeds. For milk traits in dairy cattle there are substantial heterosis estimates between exotic and tropical breeds (Rege,

1998) and there have been recommendations to use these through rotational cross-breeding (Gregory and Trail, 1981; Thorpe *et al*., 1993). Rotations are most interesting for dairy cattle as these generally have the lower reproduction performance. Except for some cross-breds among Criollo (taurine breeds) and *Bos indicus* breeds in Latin America (Plasse, 1988), we know very little about heterosis in crosses among indigenous breeds. We can only speculate that they should be lower in crosses among *Bos indicus* breeds which contribute the majority of indigenous cattle in the tropics.

b. The sires used for rotation guarantee persistent heterosis.

Within breed variation of livestock in developing countries is usually much higher than in temperate breeds. If heterosis is found in cross-breeding experiments among specific indigenous breeds, we should be sure that these can be repeated. The breeds involved should be structured so that herds or flocks are available from which sires with high genetic merits and a reliable genetic uniformity can be selected.

c. Controlled mating and dam identification are required to apply systematic rotation.

Optimal use of additive breed and heterosis effect is hard to achieve in extensive livestock grazing systems. This is even difficult in most husbandry conditions of advanced livestock industries in developed countries. Systematic rotation should guarantee that e.g. sires of breed A should be mated to a dam ($^1/_3$A $^2/_3$B) in a two-breed rotation and to dam ($^1/_7$A $^2/_7$B $^4/_7$C) in a three-breed rotation.

d. If controlled mating is not possible, breeds of sire should be mated periodically.

Periodic mating of sires means that in each mating period or in consecutive mating periods only one breed of sire is mated to the cross-bred females. Then dams should be marked according to their sire. This indicates the gene fractions of sire breeds in each dam. The sires in a given mating period, say those of breed A, will then mate two groups of dam, namely ($^1/_3$A $^2/_3$B) and ($^2/_3$A $^1/_3$B) in a two-breed rotation and the three groups ($^1/_7$A $^2/_7$B $^4/_7$C), ($^1/_7$B $^2/_7$C $^4/_7$A) and ($^1/_7$C $^2/_7$A $^4/_7$B) in a three-breed rotation. Only offspring of those dams with the least gene proportion of breed A, namely of dams ($^1/_3$A $^2/_3$B) and ($^1/_7$A $^2/_7$B $^4/_7$C) will be the correct ones for replacement, i.e. those with the highest heterosis. The others should be slaughtered. This guarantees the same maternal heterosis as in controlled matings. If dam identification is not possible, periodic mating of sires in consecutive years should still be applied because the majority of dams mated has a low gene proportion of the breed of sire due to the age structure of dams.

e. Terminal rotation seems advantageous but is hard to manage.

Terminal sires mated to dams from rotational cross-bred generations result in the utilisation of complementary and more direct heterosis.

Problems are the same as those discussed for terminal two-way crossing. The greatest handicap is the risk of replacement due to small herd / flock sizes. Furthermore, there should be sires of at least three breeds instead of two for which carefully controlled mating is required.

f. Rotation with generation preference is very efficient if controlled mating is possible.

The option of generation preference is most interesting for a two-breed rotation. If one of the breeds involved has a superior maternal performance (say breed A), the rotational cross-bred generation with the higher gene proportion from A should be preferred in size. With controlled mating, dams of this generation ($^2/_3$A $^1/_3$B) are mated to sires of breed B (assumed to be better in meat) so that complementarity can be used to a large extent. Replacement conditions are much better than in two-way crosses or in terminal rotation. Whereas there the maximal capacity for terminal crossing was 1-2 / n, here the maximal proportion of the better "dam generation" ($^2/_3$A $^1/_3$B) is 1-2 / (2+n). The figure n is the number of offspring reared per dam of the other generation ($^1/_3$A $^2/_3$B). For n = 2, 3, 4, 5 or 6 this means a proportion of 50, 60, 67, 71 and 75 percent, respectively.

g. Rotations without controlled mating are not recommended if composite breed formation is possible.

At a first glance, periodic sire rotation without controlled mating seems attractive for extensive grazing systems. It can be easily handled and applied in a single farm or unit whenever appropriate pure-bred sires of the breeds involved are available. A problem may be the cost of sires. As only one sire breed is mated each period or in consecutive mating periods, the sires of the other breed or breeds have to be kept inactive until the next season or sold after a limited time of use. The benefits from heterosis are not much higher than from blending the breeds involved in a synthetic breed. Once consolidated, the handling of a composite breed is much easier. The formation of composites, however, is a matter beyond the facilities of a single farm or unit. Whenever the conditions and prerequisites mentioned previously exist (see Chapter 5.1), cooperation in a composite breed formation programme is recommended.

6. Final remarks

This paper was intended to deal with opportunities of exploiting benefits from cross-breeding in low to medium input grazing systems. While we restricted to crossing among only indigenous breeds, there is no doubt that at least with a medium input environment, temperate breeds could be considered as partners as well. The inclusion of temperate breeds is the issue of another paper. The limitation to indigenous genetic resources means lower risk since indigenous breeds are assumed to have the bonus of some adaptation to the various stress factors of the tropics.

In the social, economic, infrastructural and institutional framework of livestock production in developing countries, there are many obstacles to the introduction of any breeding strategy. The importance of risk prevention is one of them, the frequent lack of cash economy and market-orientation is another. Although it is certain that a great variety in the genetic value of indigenous genetic resources exists, this is hard to exploit through cross-breeding. In contrast to temperate breeds, so-called breeds in the tropics are genetically not consolidated, they are usually not recorded, not structured and seedstock producers such as in temperate breeds who could guarantee quality and uniformity of genetic material are not available. There are seldom breeding societies or other institutions responsible for genetic and administrational activities for a breed and properly educated personnel are not available or cannot be paid.

The availability of superior indigenous breeds, at least for special traits, is a prerequisite of utilising genetic variety through cross-breeding. Therefore, there is an urgent need for an international programme for coordinated genetic evaluation, testing and preparation of designed germplasm and animals from superior indigenous breeds for special needs and environments in the tropics.

Independent of the situation in developing countries, controlled mating in grazing herds or flocks is generally hard to manage. This automatically excludes some of the systematic cross-breeding systems. Generally, there may be arguments against all of the cross-breeding systems discussed in this paper. The formation of composites requires a certain size and may thus not be flexible enough as even small geographic areas will include stockholders with widely different environmental conditions. The other systems are free of this disadvantage. They can be used and managed according to the specific needs of the individual herd or flock but they require an owner or manager with a high amount of operational skills. The most interesting seem to be stratified cross-breeding systems. They can best include the use of low-input requiring and highly adapted pure-breeds and thus contribute to maintain sustainable agriculture. Mating within the herds/flocks participating in the stratification is easy but the system requires a degree of readiness for cooperation between units which is hard to be realised. Rotational systems will generally fail due to the need for controlled mating. Rotation without controlled mating might be interesting in certain conditions, but the use of cross-breeding effects is only marginally superior to those of a composite breed.

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