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Review article

Conserving domestic animal diversity among composite populations

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Abstract

The erosion of domestic animal diversity due to natural causes and creative human activity is of serious concern if current production levels are to be sustained and the changing demands of future markets are to be addressed. The application of quantitative genetic principles that have proven to be successful in the genetic improvement of livestock and poultry species has made it possible to combine endangered landrace, population or breed with one or more established breeds into multi-breed (composite) populations for specific objectives. The formation of composite populations does not directly increase the number of animals in breeds under threat of being endangered or extinct. However, the high productivity of the newly developed composite population not only promotes the conservation of the inherent potential in some rare breeds with considerable genetic merit but can ensure their utilization to satisfy varying husbandry practices, marketing forces and consumer preferences for future markets of animals and animal products. The higher reproductive rate and lower generation interval are performance traits of economical importance to breed formation in sheep and goats where a larger number of breeds are associated with some degree of risk and declining at rates that may reach critical levels in the near future. The Finnish Landrace sheep, outstanding in fecundity, first brought to attention in 1963 has since been imported by more than 40 countries and combined with breeds established in the country to form composite populations contributing towards substantial reduction in ewe costs per unit of lamb marketed. This is a typical example of conservation with utilization. In the past centuries, more than 443 composite breed populations of sheep have been developed in 68 countries. At the same time in goats, there are more than 80 composite breed populations in 37 countries. Finally, the enhanced production efficiencies in the newly developed composite population provide an opportunity for exploiting genetic diversity to the benefit of the livestock and poultry industries, and at the same time conserving the inherent potential of the foundation breeds.

Keywords: Conservation; Endangered breeds; Crossbreeding; Breed formation; Selection

1. Introduction

Major achievements in the field of animal breeding have come from the application of quantitative

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genetic principle that has demonstrated success in the improvement of livestock and poultry species. These advances include breed evaluation; crossbreeding; formation of multi-breed (composite) populations; selection indices based on phenotypic, genetic and economic parameters; the use of multiple trait mixed model methodologies to estimate genetic parameters; and the simultaneous estimation of the breeding values of parents and their offspring for the identification of individuals with potential merit for genetic improvement. In recent decades, there has been a revival of interest in the creation of composite populations from crossbred foundation, with the aim of exploiting production efficiency to the benefit of the livestock and poultry industries. However, the present methods differ from the older ones principally in their more intensive and deliberate application of genetic knowledge. The concept of composite populations has been an integral part of the breeding schemes employed in beef cattle (Vianna and Jondet, 1978; Cundiff and Gregory, 1999; Gregory et al., 1999), dairy cattle (Wellington and Mahadevan, 1977; Alexander et al., 1984), sheep (Winters, 1953, 1954; Maijala and Terrill, 1991; Shrestha and Heaney, 2003, 2004), pig (Rempel and Maijala, 1991) and poultry (Crawford, 1990) breeding industries for the production of crossbred commercial breeders used for the production of fiber, meat, milk and egg.

Prospects for complementing any endangered landrace, population or breed with one or more established breeds into a multi-breed population present considerable interest. Although, the development of a composite population does not directly lead to the preservation of the endangered breed, it does capitalize on their inherent potential for performance traits of economical importance while promoting “conservation by utilization”. There is evidence to suggest that greater initial heterozygosity in the newly formed population, unless lost through inbreeding in the early generations, should represent higher performance and greater genetic variability for enhanced response to selection (Sumption et al., 1961). It is therefore important that a composite population be established with as broad a genetic base as possible leading to a reduction in the rate of inbreeding. This would result in increased additive genetic variance, retention of heterosis, and lower probability for the expression of lethal recessive genes. This review has been undertaken to elaborate on composite populations derived from a combination of endangered and established breeds for the conservation of domestic animal diversity and their utilization for future markets of animals and animal products.

2. Genetic resources

Domestication of the animal species probably occurred during the Mesolithic period around 8000–7000 BC (Zeuner, 1963; Ryder, 1983). Later, evolutionary forces of migration, mutation, selection, genetic drift and creative human activity jointly contributed to the origin of numerous identifiable morphological characteristics and colossal amount of variability in production performance. This has resulted in the vast array of landraces, populations and breeds that comprises domestic animal diversity. It is interesting to note that it was only in the 17th century Robert Bakewell from Dishley, England assembled animals with similar morphological characteristics into a population, and developed the foundation of pedigree breeding based on the concept of “like begets like” and “breed the best to the best” (Lush, 1945). Bakewell later established breeds of Shire horses, Longhorn cattle and Leicester sheep. Consequently, animal breeding plans based on inbreeding, prepotency, leasing of sires, progeny testing, auctions and promotion became accepted practices in the marketing of livestock and poultry. In 1822, the Coates’ Herdbook was established for Shorthorn cattle. This was followed by the registration of animal pedigrees and maintenance of herdbooks to restrict introductions and thus, the development of a large number of pure breeds. Breeders not only selected for the ideal type of animal, but promoted breeds based on excellence for what was considered desirable morphological characteristics and production performance (Lerner and Donald, 1966). At that time, the difference between purebred and grade animals was so great that every effort was made to ensure purity. This led to the dogma that all purebreds were superior animals. Concurrently, purebred livestock and poultry developed in the United Kingdom and continental Europe were exported to many countries in the world. During the colonial period following the discovery of the Americas in the 14th century, conditions of favourable climate, abundance of vegetative growth, freedom from predators and the absence of communicable diseases contributed to the rapid expansion of the animal population.

In the late 1920s, the availability of purebred breeding stock was adequate to supply the needs of the breeders. This was followed by a gradual decline in the number of registrations. Following World War II, the economic pressure for producing cheap commodities to meet the growing demand of the increasing human population put more emphasis on the need to improve productivity. Many breeds were evaluated for productivity and those that failed to meet the performance criteria were discarded in favour of those that were more productive. Canada has been part of the worldwide trend towards concentration on a few breeds, lines or strains for the production of commercial stocks.

The characterization of all the livestock and avian species in the world could lead to the identification of populations that are not only more effective in resource utilization but are also adapted to extreme agro-ecological zones. They may possess the potential for increased production efficiency and add value to animal-based products. Consequently, there has been a continual effort to develop an inventory, and to document the origin, distribution, adaptability, morphological characteristics and production performance of domestic animal genetic resources (Phillips et al., 1945; Mason and Maule, 1960; Epstein, 1969, 1974, 1977; Cockrill, 1974; Dmitriev and Ernst, 1989; Simon, 1990; Simon and Buchenauer, 1993; Gall, 1996; Mason, 1996; Scherf, 2000). The Global Databank for Farm Animal Genetic Resources includes 6379 breed populations comprised of 30 mammalian and avian species (Scherf, 2000). According to Oldenbroek (1999), there are 332 cattle, 407 sheep, 123 goat, 156 pigs and 213 horse breeds presently maintained in the 37 European countries. The most recent estimates of domestic animal genetic resources in Canada include 58 breeds of horses, 54 breeds of cattle, 41 breeds of sheep, 14 breeds of goats and 14 breeds of swine (Shrestha, 1995). In the absence of herdbooks to ensure the purity of the breeding animals, which is the case in many developing countries, there is the distinct possibility that a number of indigenous populations may represent landraces or isolated self-contained breeding population that do not have distinctive characteristics. This represents a serious drawback to ensuring purity of breeds when establishing distinct populations of livestock and poultry. In many countries, landraces with similar characteristics have been pooled into one breed population in order to avoid the issue. In India, the strategy employed to classify a large number of sheep and goat breeds was based on identifiable morphological characteristics that are distinct from other populations in the vicinity, particularly those with a local name (Acharya, 1982).

More recently, the promise of new methodologies to identify distinct populations has been enhanced due to considerable advances in the development of comprehensive gene maps and determination of genetic distance based on highly polymorphic microsatellite markers. Hansen et al. (2002, 2003) estimated the genetic distance among Canadienne, Brown Swiss, Holstein and Jersey cattle of Canada based on microsatellite markers and mitochondrial D-loop sequence variation. The Food and Agriculture Organization (FAO), International Livestock Research Institute (ILRI), Institut National de la Recherche Agronomique (INRA) along with many laboratories have been engaged in a global effort to establish relationships among populations of livestock and avian species. This could eventually lead to the identification of distinct populations reducing the need to preserve many breeds. Information on more indigenous breed populations in the world continues to rise and is being documented in the Animal Genetic Information Bulletin, an FAO publication.

3. Erosion of domestic animal diversity

In December 1959, the Symposium of the American Association for the Advancement of Science reviewed the status of germplasm resources in the development of the US Agriculture industry, and produced a road map for the future development and protection of these resources (Hodgson, 1961). The United Nations Conference on the Environment held in Stockholm in 1972 acknowledged the rise in the erosion of domestic animal genetic resources and the need for their conservation. Subsequently, the Food and Agriculture Organization of the United Nations in 1980 organized the Technical Consultation on Genetic Resources in Rome to address this issue. In 1992, the United Nations Conference on the Environment “Earth Summit” held in Rio de Janeiro, Brazil reiterated the importance of animal genetic resources in Agenda 21 of the United Nations Convention of Biological Diversity (BCD), which became binding following ratification by 65 countries in November of 1994. In the United States, the committee on managing global genetic resources reviewed the status of livestock genetic diversity with respect to global needs (Board of Agriculture, 1993). Concurrently, FAO launched the Global Management of Domestic Animal Genetic Resources, a special program with a framework to stimulate national participation and implement conservation activities.

Details and descriptions of many varieties, types and breeds of livestock in the world has been published (Mason, 1996). It is noteworthy that the entire world relies on 40 animal species consisting of nearly 4500 breeds for its food supply (Barker, 1999). However, according to FAO nearly 800 farm animal genetic resources have been lost and about 30% of all those remaining are associated with some degree of risk (Scherf, 2000). This indicates that animal genetic resources are declining at rates that may reach critical levels in the near future.

The industrialized nations have responded with a trend towards fewer but larger farms with only a small number of breeds or populations of animals. These animals are bred and managed for the production of commercial stock with desirable morphological characteristics and outstanding production performance. At the same time, more and more breeders of livestock and avian species want superior breeding stock to increase production from fewer animals. In the developing countries, there has been a continual effort to augment the nations' food supply by importing exotic breeds with outstanding productivity in their native country for crossbreeding with less productive indigenous populations. In these countries, the widely held consensus is that offspring in the composite populations derived from crosses between exotic breeds and indigenous populations, are more productive under local conditions and requirements (Shrestha, 1998). The increased use of artificial insemination from exotic and proven sires has resulted in successive generations of crossbreeding contributing to the grading-up of the indigenous population. This has led to the development of populations composed of variable proportions of many breeds. These activities are often unplanned and characterized by loss of adaptability, fecundity and resistance to diseases contributing eventually to lowered productivity.

In the global context, a large number of livestock and poultry populations have become endangered while many are extinct because of their failure to adapt to the changing environment, and their inability to satisfy the needs and requirements of humankind. India has even considered, under certain circumstances, the physical replacement of entire breeds as an alternative to the grading-up policy (Acharya et al., 1982). In many countries, the complete replacement or grading-up of indigenous or less productive livestock and poultry populations with more productive exotic breeds or populations is contributing to the narrowing of the genetic base and the erosion of domestic animal diversity.

Breeds maintained in small populations are subject to diseases, genetic drift, genetic bottle neck from limited numbers of parents for some generations, inbreeding depression, natural selection, contamination from other germplasm, and are costly to maintain in terms of labour and facilities. These activities are contributing to the depletion of domestic animal diversity and the vulnerability of populations to the point that presently it is of major concern to breeders of farm animals. To complicate the issue, newer technology based on advances in the synchronization of estrus, artificial insemination, embryo transfer and cloning has contributed to the ease with which rapid and successful propagation of superior germplasm can be achieved, and is further contributing to the erosion of domestic animal diversity. If current production levels are to be sustained by the animal industry, and changing demands for future markets are to be addressed, it is imperative that in situ and ex situ conservation of animal genetic resources considered endangered breeds need to be given serious consideration.

4. Development of composite population

Many composite populations were developed for experimental studies in the laboratory and have never reached commercial application. These populations utilized the well-documented quantitative genetic principles of heterosis retention, breed complementarity, and genetic variability as is evident from the breeding approaches adopted in their formation. Despite initial unfavourable effects on production performance, there is considerable merit in forming composite populations for conservation of domestic animal diversity and their exploitation for commercial purpose. The negative effect on performance is a result of random inter-breed recombination of favourable joint effects among nonallelic genes which had been fixed in the parental breeds (Dickerson, 1969), and the inability to exploit breed difference in maternal and individual performance. In sheep, the recombination effects for growth and carcass quality have been reported to be small or negligible in support of developing multi-breed populations, in contrast the same measures were negative for prolificacy and longevity (Boylan, 1985). Additional studies are necessary to determine the size of recombination loss and address this issue. Furthermore, there is a theoretical decrease in the genetic potential for commercial performance due to the lower level of heterozygosity maintained in the composite population than that of a specific breed cross or rotational crossbreeding involving the same number of breeds. Gregory et al. (1999) have reported that a substantial proportion of the heterosis for several desirable production characteristics in the single cross due to dominant gene action was retained even after many generations of *inter se* mating. It was shown to be equal to or even greater than that expected from crossbreeding in beef cattle. In theory, the loss in heterosis in the composite population can be reduced by increasing the number of breeds to be assembled to three, or four, or even more, retaining two-thirds, three-fourths, or more, average productivity of single crosses among the constituent breeds.

The majority of the newly developed composite breeds in the world were not assembled in a formal way, as would have occurred with laboratory animals. These breeds were formed by initial successes in crossbreeding followed by formation of crossbred foundation stocks that were retained by the breeders for further development. Compared to a more complex commercial hybrid approach involving many levels of crossbreeding, the managing of a single population was much simpler. In the 1940s, the University of Minnesota exploited breed differences to develop the Minnesota breeds of swine and sheep (Winters, 1953, 1954; Shrestha, 1973). To achieve genetic improvement, crossbred offspring of desirable types chosen for potential genetic merit in morphological characteristics and production performance were retained for breeding. Further crossbreeding and subsequent *inter se* mating for a few more generations followed. Extensive reviews on the development of new breeds of dairy cattle (Wellington and Mahadevan, 1977; Alexander et al., 1984; Hayman, 1977), beef cattle (Vianna and Jondet, 1978; Cundiff and Gregory, 1999), sheep (Maijala and Terrill, 1991) and swine (Rempel and Maijala, 1991) have been published.

Evaluation of breeds based on the performance of the pure breeds and their crosses or a combination of both, has provided vital information for the choice of breeds or populations that have demonstrated genetic merit for the improvement of morphological characteristics and production performance under specific feeding and management conditions. Although many breeds exist in the world, only a fraction of these have been subjected to evaluation. The majority of studies on evaluation of indigenous breeds in the developing countries are based on small numbers of animals from institutional herds. These are often confounded with feeding and management practices, which, furthermore, are inconsistent with those practiced by the producer. Because of the contrasting management practices associated with husbandry, breeding, productivity, disease, and their interacting influence on the prevailing diet and environment in the household, region and country, as well as social and cultural attributes, it is evident that complex issues are involved in the conservation of breeds of livestock and avian species. Furthermore, many indigenous populations are raised by the resource poor producers in either small or large multi-species herds. These typically involve traditional low input management, examples being nomadism and semi-nomadism in agropastoral production systems, in arid desert, and in grazing areas around urban or property boundaries (Shrestha, 2002).

Experienced breeders, besides having maintained livestock and poultry breeds for a number of years, are privy to a wealth of information on the genetic background, health status, behaviour and previously available knowledge on their performance. It is important to identify breeds and their crosses that demonstrate potential genetic merit for inclusion in a composite population, and relevant information on their genetic background, health status, behaviour and management need to be carefully examined. The strategy employed during the choice of parental breeds or populations to be assembled for developing composite populations depends largely on the availability of healthy animals of appropriate breeding age, and fiscal constraints. The latter usually results in the purchase of a limited number of unrelated animals, mostly sires (Shrestha and Heaney, 2003, 2004).

The biology of the mammalian species, particularly for multiparous animals relative to the maternal environment provided during gestation and nursing is of special significance. Not only does heterosis improve the maternal environment, it is also expected to enhance milk production in the female parent and consequently, growth performance of the crossbred offspring. The use of crossbred males has, until recently, received little attention in animal breeding. However, the possibility of paternal heterosis effects during fertilization and embryonic survival, though unlikely, should not be excluded. Here, the benefit in performance from maternal heterosis and favourable genes in the crossbred dams will not be realized. Therefore, several approaches are used in the formation of composite populations. All procedures are contingent on the number of parental breeds or populations to be incorporated, and the order of mating the specialized breeds and their crosses.

A composite population may be developed from two breeds (endangered and established) by backcrossing the two-breed cross offspring (G-I) to their purebred parent resulting in crossbred offspring (G-II) composed of 25 and 75% for the two breeds (Fig. 1). This is followed by mating of G-I to G-II resulting in G-IIIa offspring, and G-II to G-I resulting in G-IIIb offspring, composed of 37.5 and 62.5% for the two

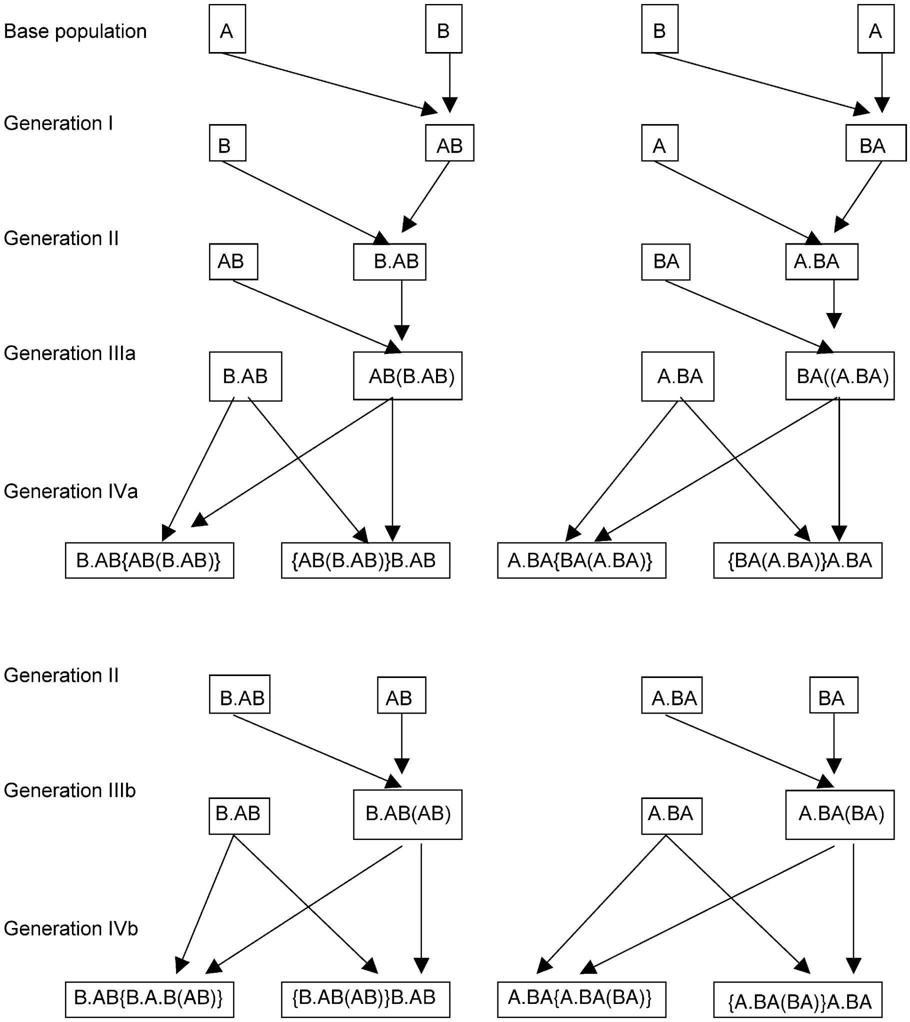

Fig. 1. Flowchart showing the various crossbred combination leading to the development of two breed (A and B) composite population.

breeds. Finally, offspring derived from reciprocal crosses of G-II and G-IIIa or G-IIIb, produce G-IVa and G-IVb offspring, composed of 31.25 and 68.75% for the two breeds. Following *inter se* mating for several generations, the proportion for the two parental breeds will eventually stabilize at one-half in the composite population.

Lauprecht (1961) proposed a procedure for the development of a composite population based on three divergent breeds consisting of backcrossing three-breed cross offspring composed of 25, 25 and 50% (G-IIa and G-IIb) to the specific two-breed cross parents (G-Ia and G-Ib), and vice versa, resulting in G-IIIa and G-IIIb offspring, composed of 37.5, 37.5 and 25% for the three breeds (Fig. 2). The proportion of breeds in the offspring varies according to the parental breed of sire and dam. The resultant crossbred (G-IIIa and G-IIIb) is again back crossed to the three-breed cross (G-IIa and G-IIb), and vice versa, resulting in G-IVa and G-IVb offspring, composed of 37.5, 31.25 and 31.25% for the three breeds. This is followed by *inter se* matings for several generations. The contribution of all the three parental breeds would eventually stabilize at one-third in a composite population.

As the newly formed population achieves uniformity following successive generations of random mating, further genetic improvement of desirable characteristics can be based on selection for optimal breeding objectives and realistic economic goals. The above approach can be used for the development of a composite population based on more than three divergent breeds. Many of the composite breed populations in the world have not been developed in a systematic manner as described earlier. Nevertheless, there is opportunity for greater probability of success in a planned approach due to the possibility of simultaneous evaluation of breed combinations during breed development and prospect for adjustment, if required. As the number of breeds to be combined into a composite population increases, management of offspring consisting of various crossbred combinations can become a real challenge. Nevertheless, the number of cross combinations can be reduced if the use of crossbred sires can be avoided, thereby reducing the resource requirement for breed formation. The concept of composite breed development in small ruminants is feasible because of the high reproductive rate and lower generation interval.

5. Evolution of composite sheep breeds

In the 18th and 19th centuries, the raising of sheep in the world was more or less traditional and under conditions of sedentary, nomadic and semi-nomadic management. A number of sheep breeds evolved in the desert, tropical, temperate and mountainous regions of the world where rainfall, wind, temperature, solar radiation and vegetation varied. During this period, increased emphasis was placed on conformation, hardiness and productivity invigorating interest in the development of new sheep breeds derived from a combination of two or more breeds. The registered breeds such as the Leicester and Merino exceeded grade sheep in performance and were therefore considered as a source of breeding animals to many flocks in the world. Following the Second World War, there was economic pressure for producing cheaper commodities to meet the growing demand of the increasing human population and the need for more emphasis to improve production efficiency. At the same time, the contribution of wool towards productivity declined in many countries due to the changing consumer preference in favour of synthetic fibre and more emphasis was placed on raising sheep for their meat, milk and fur. The influence of marketing forces resulted in the development of 443 composite breed populations of sheep in 68 countries, all derived from two or more distinct breeds, populations and landraces (Table 1).

In North America, producers opted out of traditional sheep farming in favour of family farms. The increased requirement for investment in housing, feeding, labour and disease control made it necessary to integrate intensive system that would improve efficiency of production. This stimulated interest in the development of new breeds that could possibly approach potential biological ceiling based on a wealth of knowledge and skill of the breeder, newly identified breeds with potential genetic merit as well as advances in the application of quantitative genetic methodologies. The breeds chosen world wide for potential genetic merit were the Dorset, Suffolk and Texel for meat, the Finnish Landrace, Romanov and Booroola for fecundity, the Merino and Rambouillet for wool, the Karakul for fur, and the Awassi and East Friesian for milk.

In the late 1960s, the sheep breeds established in North America lacked the inherent potential for increased fecundity, lean muscle yield and milk produc-

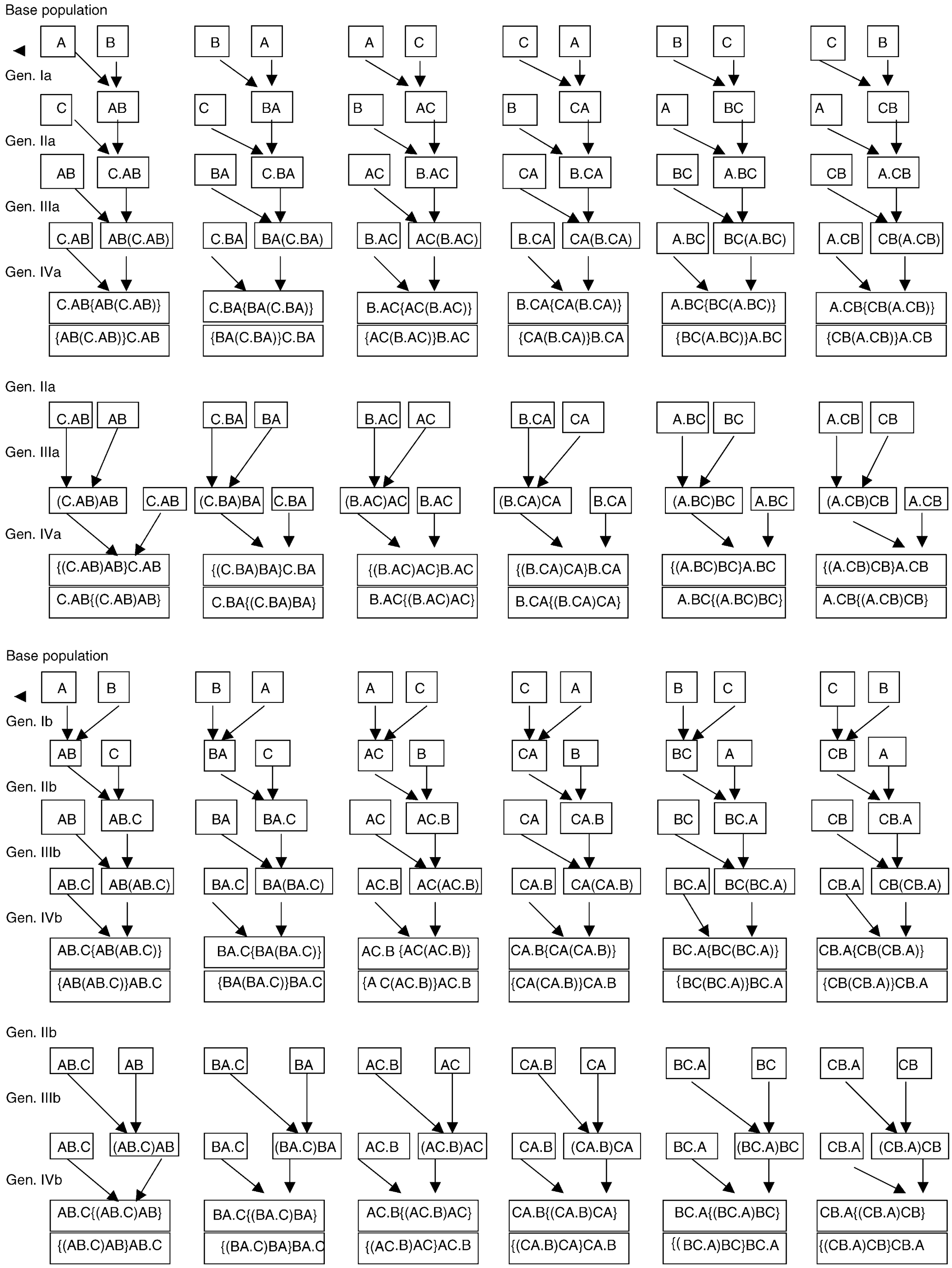

Fig. 2. Flowchart showing the various crossbred combination leading to the development of three breed (A–C) composite population.

Table 1
Composite breed population of sheep that have been developed in the world, number of foundation breeds and the year of origin or year recognized by country of origin

Country	Composite breed population	No. of foundation breeds[a]
Algeria	Tadmit	2 (1925)
Argentina	Argentine Cormo	4 (1979)
	Corino	2 (1970)
	Pampinta	2 (1980)
Armenia	Armenian Semicoarsewool	3
	Kyasma	2
	Martunin	3
Australia	BLM	2 (1955)
	Bond	3 (1909)
	Booroola Leicester	2
	Borino	2
	Bumfdale	5 (1979)
	Bundoran Comeback	2 (1971)
	Bungaree Merino	2
	Comeback	2 (1976)[b]
	Coolalee	6 (1968)
	Cormo	2 (1960)
	Daldale	3 (1970)
	Dormer	2
	Elliotdale	4 (1963)
	Fonthill Merino	2 (1954)
	Glenara Improver	3
	Gromark	2 (1979)[b]
	Hyfer	3 (1978)
	Improved Border Leicester	2
	Meridale	24
	Poll Dorset	2 (1954)[b]
	Polwarth	2 (1880)
	Romshire	2
	Waridale	3 (1970)
	White Suffolk	3 (1977)
	Zenith	2 (1947)
Austria	Austrian Negretti	2+
	Carinthian	3 (1988)[b]
Azerbaijan	Azerbaijan Mountain Merino	3 (1947)
Brazil	Brazilian Somali	2 (1939)
	Brazilian Woolless	2
	Rabo Largo	2
	Santa Ines	2 (1940)
Burkina Faso	Mossi	2
Bulgaria	Bulgarian Dairy	2 (1970)
	Danube Finewool	4 (1950)
	Karnobat Finewool	2 (1950)
	Mountain Tsigai	3 (1950)
	North Bulgarian Semifinewool	6
	North-East Bulgarian Finewool	4 (1950)
	Petrokhan Tsigai	3
	Pleven Blackhead	2
	Razlog	3 (1955)
	South Bulgarian Semifinewool	4
	Thrace Finewool	6 (1943)
	White Klementina	3 (1916)
	Zlatusha	3 (1965)
Cameroon	Maroua	2
Canada	Canadian Arcott	12 (1988)[b]
	Canadian Corriedale	3 (1919)
	DLS	3 (1989)
	Outaouais Arcott	9 (1988)[b]
	Newfoundland	7 (19th)
	Rideau Arcott	9 (1988)[b]
	Romnelet	2 (1935)
China	Aohan Finewool	3 (1970)
	Chinese Karakul	3 (1960)
	Chinese Merino	3
	Erduos	3
	Gadasu	2 (1970)
	Gansu Alpine Finewool	6 (mid 20th)
	Guizhou Mutton-Wool	5
	Inner Mongolian Finewool	2
	Jia Shike	2 (1970)
	Lanzhou Large-tail	2 (1862)
	Linchuan	3
	Ningxia Black	2
	North-East China Finewool	3
	North-East China Semifinewool	2
	Qinghai Semifinewool	4
	Shanxi Finewool	2 (1920)
	Sichuan Semifinewool	4 (1970)
	Tibegolian	2
	Xinjiang Finewool	4 (1935)
	Yunan Semifinewool	2 (1970)
Colombia	Manchada Paramuna	2 (1976)
Croatia	Dubrovnik	2 (late 18th)
	Island Pramenka	2
	Pag Island	2 (19th)
Czeck Republic	Improved Valachian	4
	Sharka	5
Denmark	Danish Finewool	2
	Danish Landrace	4 (1900)
	Såne	3 (1991)
Egypt	Ossimi-Finn	2 (1980)
	Rahmani-Finn	2 (1980)
Estonia	Estonian Darkheaded	2 (1940)
	Estonian Whiteheaded	2

Table 1 (*Continued*)

Country	Composite breed population	No. of foundation breeds[a]
France	Avranchin	4 (1928)[b]
	Berrichon du Cher	6 (1936)[b]
	Blanc du Massif Central	2 (1965)
	Bleu du Maine	3 (1938)[b]
	Boulonnais	3 (1963)
	Catalan	4
	Central Pyrenean	2
	Charmoise	5 (1896)[b]
	Charollais	2 (1963)[b]
	Cotentin	2 (1925)[b]
	French Alpine	2 (1952)[b]
	FSL	3 (1967)
	Ile de France (Dishley Merino)	2 (1922)[b]
	INRA 401	2 (1980)
	Landais	2
	Lourdais	2 (1975)[b]
	Rayole	2 (1980)
	Roussillon Red	3
	Roussin de la Hague	4 (1983)
	Trun	2 (1960)
Georgia	Georgian Fat-tailed Finewool	3 (19th)
	Georgian Semifinewool Fat-tailed	4 (1931)
Germany	Bentheimer	2 (1934)[b]
	German Blackheaded Mutton	4 (1920)[b]
	German Karakul	2
	German Mountain	3 (1938)[b]
	German Whiteheaded Mutton	3 (1885)[b]
	Leine	5 (1906)[b]
	Merino Longwool	3 (1971)
	Merinolandschaf	2 (1922)[b]
Ghana	Nungua Blackhead	2
Greece	Argos	2
	Evdilon	2
	Frisarta	4 (1946)
	Moraitiko	2
	Mytilene	2+
	Rhodes	2
Greenland	Greenland	2
Hungary	Csenger Merino	2 (1982)
	Hungarian Merino	7
	Hungarian Prolific Merino	2 (1992)
	Kazanluk Semifinewool	5 (1964)
	J-AKI-1	2 (1980)
	J-AKI-2	3 (1980)
	Prolific Babolna	3 (1970)
	Tetra	3 (1960)
Iceland	Kleifa	3
India	Avikalin	2 (1970)
	Avivastra	2

Table 1 (*Continued*)

Country	Composite breed population	No. of foundation breeds[a]
	Baghdale	3
	Bharat Merino	5 (1980)
	Hissardale	2 (19th)
	Kashmir Merino	7 (1947)
	Nilgiri	4 (18th)
	Raymond Merino	5 (1973)
	Sandarsamand	2 (1935)
	Sandyno	2 (1973)
	UAS	3
Indonesia	Priangan	3 (19th)
Ireland	Belclare Improver	4 (1985)[b]
	Fingalway	2 (1970)
	Finn-Dorset	2
	High Fertility	6+ (1965)
	Improved Galaway	2
Israel	Assaf	2 (1955)
	Israeli Improved Awassi	2 (1943)[b]
Italy	Apennine	3 (1981)[b]
	Campanian Barbary	2 (1971)[b]
	Comisana	2 (1942)[b]
	Cornigliese	3
	Fabrianese	2 (1974)[b]
	Finarda	2
	Gentile di Puglia	4 (1942)[b]
	Mascherina	2
	Segezia Triple Cross	3
	Sicilian Barbary	2 (1942)
	Sopravissana	5 (1942)
	Tyrol Mountain	3
Kazakhstan	Aktyubinsk Semicoarsewool	2
	Chuisk Semifinewool	4
	Degeres Mutton-Wool	3 (1931)
	Edilbaev	2
	Kargalin Fat-rumped	4
	Kazakh Arkhar-Merino	2 (1934)
	Kazakh Corriedale	3
	Kazakh Finewool	3 (1946)
	Kazakh Semifinewool	5 (1945)
	North Kazakh Merino	2 (1976)
	South Kazakh Merino	6 (1966)
	West Kazakhstan Mutton-Wool	5 (1952)
Kyrgyzstan	Kirgiz Fat-rumped	3
	Kirgiz Finewool	4 (1956)
	Tyan Shan	5 (1966)
Latvia	Latvian Darkheaded	4 (1937)
Libya	Barbary Halfbred	2
	Ghimi	2
Lithuania	Lithuanian Blackheaded	3 (1923)

Table 1 (*Continued*)

Country	Composite breed population	No. of foundation breeds[a]
Mexico	Chiapas	5
	Tarset	2
Mongolia	Aohan Finewool	3 (1970)
	East Mongolian Semifinewool	4 (1962)
	Hangay	2
	Orhon	4 (1943)
	Sumber	2 (1950)
	Torguud	2 (1962)
	Yoroo	4 (1981)
Morocco	South Morroccan	2
	Timahdit	3
	Zaian	2
	Zoulay	2
The Netherlands	Dutch Black Blaze	4 (1979)[b]
	Flevoland	2 (1975)
	North Holland	2 (1970)
	Rijnlam A	2
	Rijnlam B	3
	Schoonebeker	2 (1990)[b]
	Swifter	2 (1967)
	Texel	3 (1909)[b]
New Zealand	Borderdale	2 (1930)
	Border-Merino	2
	Border-Romney	2
	Carpetmaster	3
	Cheviot-Corriedale	2
	Coopworth	2 (1968)[b]
	Corriedale	2 (1910)[b]
	Elliotdate	4 (1960)
	New Zealand Halfbred	4
	New Zealand Wiltshire	2 (1974)
	Perendale	2 (1961)[b]
	Romney-Corriedale	2
	Skye Farm Romney	3 (late 1960)
	South Dorset Down	2
	South Hampshire	2 (1970)
	South Suffolk	2 (1938)
Nigeria	Permer	2
	Yankasa	2
Norway	Dala	3 (1926)[b]
	Norwegian Fur sheep	2 (1968)[b]
	Rygja	3 (1926)[b]
	Steigar	2 (1954)
Pakistan	Baghdale	3
	Pak Awassi	2
	Pak Karakul	2 (1965)
Peru	Asblack	3 (1990)
	Junin	5 (1940)
Philippines	Laguna	2
Poland	Bialystok	2 (1963)
	Bochnia	2
	Damline 66	3 (1980)
	Damline 77	3 (1980)
	Friserra	2 (1960)
	Jędrzychowice Merino	2 (1954)
	Kamieniec	3 (1954)
	Koszalin	4
	Lublin	3 (1950)
	Olkusz	2
	Polish Blackheaded Mutton	4 (1976)
	Polish Corriedale	2 (1962)
	Polish Longwool	5
	Polish Lowland	9
	Polish Merino	2 (1952)
	Polish Mountain	3 (1946)
	Polish Strongwooled Merino	3
	Polish Whiteheaded	6 (1976)
	Pomeranian	4 (1984)
	Prolific 09	3 (1976)
	Prolific meat 08	5 (1976)
	Prolific meat 10	8 (1976)
	Prolific wool 04	2 (1976)
	Sireline	5 (1970)
	Silesian	2 (1932)
	Wielkopolska	2 (1977)[b]
	Żelazna	3 (1955)
Portugal	Bordaleiro	2
	Fonte Bôa Merino	2 (1902)
	Friserra	2 (1962)
	Portuguese Merino	4 (1929)
Romania	Bîrsa	3 (1953)
	Danube Merino	2
	Palas Merino	6 (1926)[b]
	Ruşeţu 1	3
	Spancă	2
	Stogoşă	2
Russia	Altai	4 (1940)
	Altai Mountain	3 (1945)
	Angara Merino	3 (1974)
	Caucasian	3 (1921)
	Chita	2
	Dagestan Mountain	2 (1926)
	Gorki	2 (1950)
	Grozny	2 (1929)
	Kalinin	2 (1935)
	Karachai Mountain Mutton-Wool	3
	Krasnoyarsk Finewool	5 (1963)
	Kuchugury	2 (1970)
	Kuibyshev	2 (1938)
	Kulunda	3

Table 1 (*Continued*)

Country	Composite breed population	No. of foundation breeds[a]
	Liski	2 (1936)
	Manych type of Stavropol	2
	North Caucasus Semifinewool	3 (1944)
	North Caucasus Mutton-Wool	3 (1944)
	Omsk Semifinewool	2
	Oparino	2
	Ostrogozhsk	2 (1963)
	Pechora	2 (1937)
	Russian Longwool	2 (1978)
	Russian Mountain Merino	2
	Salsk	2 (1932)
	Siberian Merino	5 (20th)
	Siberian type Soviet Mutton-Wool	3
	Soviet Merino	6 (1938)
	Soviet Mutton-Wool	5 (1950)
	Stavropol	4 (1950)
	Transbaikal Finewool	6 (1927)
	Volgograd	6 (1978)
	Vyatka	2 (1936)
Serbia	Vojvodina Merino	2 (19th)
Senegal	Warale	2 (1975)
Slovakia	Improved Valachian	4
	Slovakian Merino	3
	Solčava	3 (1983)[b]
South Africa	Afrino	3 (1969)
	Bezuidenhour Africander	3 (1918)
	Dohne Merino	2 (1940)
	Dormer	2 (1941)
	Dorper	2 (1950)[b]
	South African Merino	5 (1906)[b]
	Van Rooy	3 (1948)[b]
	White Dorper	2 (1960)[b]
	White Wooled Mountain	3 (1942)
Spain	Basco-Béarnais	2 (1960)
	Mestizo Entrefino-fino	2
	Ripollesa	2
	Salz	2 (1970)
	Talaverana	3 (1960)
Sudan	Ingessana	2
	Meidob	2
	Toposa	2
Switzerland	Engadine Red	2 (1985)[b]
	Swiss Brownheaded	2 (19th)[b]
	Swiss Charollais	2 (1991)[b]
	Swiss White Alpine	2 (1936)
Togo	Vogan	2
Tajikistan	Darvaz Mountain Mutton-Wool	3 (1948)
	Pamir Finewool	2
	Tajik	3 (1963)

Table 1 (*Continued*)

Country	Composite breed population	No. of foundation breeds[a]
Tunisia	Sidi Tabet cross	2
	Tadmit	2 (1925)
	Thibar	2 (1945)[b]
	Tunisian milk sheep	2
Turkey	Acipayam	3
	Çandir	3
	Central Anatolian Merino	2 (1952)
	Kamakuyruk	2
	Kivircik	2
	Karacabey-Merino	2 (1928)
	Menemen	3
	Menemen Kivircik	2
	Ramliç	2 (1969)
	Tahirova	2 (1964)
	Türkgeldi	3
Ukraine	Azov Tsigai	2
	Askanian Blackheaded	4
	Askanian Corriedale	2
	Askanian Crossbred	3
	Large Karakul	2 (1932)
	Multifoetal Karakul	2 (1935)
	North Ukrainian Semifinewool	4
	Transcapathian Finewool	4
	Ukrainian Mountain	2 (1950)
United Kingdom	ABRO Damline	4 (1967)
	Black Leicester Longwool	2 (1986)[b]
	Boreray	2 (1930)
	British Milksheep	5^+ (1970)
	Cadzow Improver	2 (1960)
	Cambridge	9 (1969)[b]
	Castlemilk Moorit	3 (1974)[b]
	Chevaldshay	2
	Clun Forest	3 (1865)
	Colbred	4 (1962)[b]
	Cotswold	2 (1862)
	Crickleg Barrow	2 (1970)
	Dalesbred	2 (1930)
	Dartmoor	2 (1909)
	Derbyshire Gritstone	2 (1892)[b]
	Devon, Cronwall Longwool	2 (1977)
	Devon Closewool	2 (1923)[b]
	Dorset Down	2 (1906)[b]
	Dorset Horn	2 (1862)
	English Halfbred	2 (1981)[b]
	Greyface Oldenbred	2
	Hampshire Down	3 (1889)[b]
	Kent Halfbred (South England)	2 (1988)[b]
	Lincoln Longwool	2 (1892)[b]
	Llanwenog	2 (1963)[b]
	Lleyn	3 (1970)[b]
	Masham	2
	Meatlink	5 (1963)
	Norfolk Horn	4 (1978)[b]
	North of England Mule	2 (1980)[b]

Table 1 (*Continued*)

Country	Composite breed population	No. of foundation breeds[a]
	Oldenburg	2
	Oxford Down	3 (1951)
	Pettadale	2 (1959)
	Romney Halfbred	2
	Scotch Halfbred	2
	Scotch Mule	2 (1986)[b]
	Scottich Greyface	2
	Scottish Masham	2
	Shetland-Cheviot	2
	Speckled Halfbred	2
	Suffolk	2 (1810)
	Texel-Oxford	2 (1970)
	Wealdon Four-quarter	6 (1971)
	Welsh Bleu	4 (1990)[b]
	Welsh Halfbred	2 (1955)[b]
	Welsh Masham	2
	Welsh Mule	2 (1979)[b]
	Welsh Oldenbred	2
	Wensleydale	2 (1876)
	White Face Dartmoor	2 (1951)[b]
	Wiltshire Horn	2 (1923)[b]
USA	California Red	2 (1971)
	Columbia	2 (1942)[b]
	Columbia-Southdale	2 (1943)
	Combo-6	6 (1970)
	Debouillet	2 (1954)
	Fannin sheep	2
	Katahdin	3 (1957)
	Montadale	2 (1933)
	MARC composite dam line 1	3 (1984)
	MARC composite dam line 2	3 (1984)
	MARC terminal sire composite	3 (1986)
	Minnesota 100	3 (1941)
	Minnesota 102	4 (1949)
	Minnesota 105	3 (1949)
	Morlam	8 (1961)
	Multinipple	4 (1923)
	Polypay	4 (1979)[b]
	Romeldale	2 (1915)
	Santa Cruz Island	3 (1920)
	Targhee	3 (1951)[b]
	Thribble Cross	3 (1903)
	Warhill	5
	Willamette	3 (1952)
Uruguay	Merilín	2 (1910)
Uzbekistan	Akhangaran Mutton-Wool	3
	Uzbek Mutton-Wool	3 (1955)
Yugoslavia	Birka	2
Zimbabwe	Wiltiper	2 (1946)

Source: Fogarty et al. (1984); Maijala and Terrill (1991), Mason (1996); Leymaster (1991).

[a] Year of origin or year recognized.

[b] Year breeds society, association or stud book was established.

tion. Besides, the low heritability estimates for fertility and prolificacy excluded selection as a breeding methodology for achieving genetic response in reproduction rate. At the same time, there was agreement among breeders that crossbreeding was an effective breeding methodology for exploiting the genetic potential of exotic breeds in order to achieve rapid and permanent improvement of reproduction rate in sheep (Turner, 1969). The Finnish Landrace was identified as a highly fecund sheep breed with considerable potential for improving reproduction (Donald and Read, 1967; Maijala, 1967). Later, more exotic breeds were identified world wide as a potential source for genetic improvement of sheep (Maijala, 1974; Maijala et al., 1984). Besides, the possibility for their importation without jeopardizing the health of livestock in Canada became an attractive proposition to double or triple lamb production per ewe (Shrestha et al., 1982). This resulted in the importation of the Finnish Landrace, Ile de France and East Friesian breeds in the 1960s and 1970s, all contributors to the newly developed Arcott breeds of sheep. The crossbreeding evaluation of Finnsheep and some US breeds for market lamb production concluded that sheep producers can increase the profit margin from both breed superiority and hybrid vigour of crossbred ewes and their lambs (Dickerson, 1977). In general, the use of half Finnsheep crosses with Dorset, Suffolk, Targhee or Rambouillet as commercial ewes mated with meat breed sires was expected to reduce ewe costs per pound of market lamb by 20–25% per bred ewe. Again the use of quarter Finnsheep ewes was expected to add about 20 lambs born alive per 100 ewes above domestic crossbred ewes. Under poor range conditions and with severe climatic exposure at lambing, quarter Finnsheep ewes could raise nearly as many lambs as half Finnsheep ewes and have a longer productive life. Evidence suggesting crossbreeding was an effective procedure for exploiting the inherent potential of highly prolific breeds was reported (Jakubec, 1977; Meyer et al., 1977; Smith et al., 1979). Concurrently, many new breeds of sheep were developed in the world that included contribution from the Finnish Landrace and Romanov breeds (Land and Robinson, 1985; Maijala and Terrill, 1991; Fahmy, 1996). Later in the 1990s, the Romanov and Texel breeds were imported into North America from continental Europe.

In the USA, the Polypay breed was developed with a potential reproductive capacity to exceed the Western range sheep by producing two paying crops, one for wool and two lamb crops each year (Hulet et al., 1984). The Rambouillet and Targhee breeds were chosen for hardiness, large body size, extended breeding season, herding instinct and fleece characteristics; the Doset breed for carcass quality, milking ability and long breeding season; and the Finnish Landrace for early puberty, early postpartum fertility and high lambing rate. Following reciprocal crosses between the Dorset × Targhee breed and the Finnish Landrace × Rambouillet breeds in 1970, the four breed cross was mated *inter se* and selected for high lifetime prolificacy, large lamb crop at 1 year of age, ability to lamb more frequently each year, rapid growth rate and desirable carcass quality. A typical mature Polypay ewe of moderate size produced 4.2 kg of 58s spinning count wool while the weaning age, growth rate, meat-type conformation and body condition score was comparable with or superior to the Rambouillet and Targhee breeds, and various crosses at the US Sheep Experiment Station.

In France, Ricordeau et al. (1978) reported on the advantage of the Romanov breed and their crosses in the genetic improvement of reproductive and maternal performance in sheep. In 1969, the Berrichon du Cher and Romanov breeds that excelled in carcass quality and reproductive rate, respectively, were chosen for the development of the INRA line 401 sheep (Razungles et al., 1985). The crossbred offspring were mated *inter se* for four generations in an accelerated lambing program. In the subsequent generations, the criterion for selection comprised of a fecundity index based on prolificacy of the ewe, and litter size records on those of the full and half sibs, dam and daughters. Although, coloured fleece in the new breed was considered undesirable, there was opportunity for reducing their frequency in the future by using more homozygous white rams for breeding. Nevertheless, there was interest in increasing fecundity and lamb growth to complement with the ability of ewes to raise two or three lambs under prevailing management. The productivity of the INRA line 401 was comparable to the Mérinos d'Arles in the first mating at 1 year of age and subsequent mating 8 month later while the carcass quality exceeded the cross between the parental breeds.

In Canada, the East Friesian, Finnish Landrace and Ile de France breeds from continental Europe with inherent potential for increased productivity were imported and assembled with the Corriedale, Dorset, Leicester, Lincoln, North Country Cheviot, Romnelet, Shropshire, Southdown, and Suffolk breeds established in North America to develop multi-breed synthetic populations (Shrestha and Heaney, 2003, 2004). In 1972, the genetic base of the newly formed population was closed to any further introduction of new breeding animals. Artificial lighting regimens and exogenous hormones were utilized to synchronize estrus in ewes housed indoors year-round and bred at 4-month intervals in 8-month breeding cycles. All lamb were raised from birth artificially on milk replacer and fed high energy diets, to allow for maximum expression of their genetic potential, while adult sheep were fed diets to meet nutritional requirements according to stage of production. Sheep were selected over 20 years for growth and reproductive performance leading to the development of one specialized meat-type terminal sire (Canadian Arcott) and two fecund-type dam (Outaouais and Rideau Arcotts) breeds.

The Finnish Landrace, a little known breed with outstanding fecundity since first brought to attention in 1963 (Donald and Read, 1967; Maijala, 1967) has been imported by more than 40 countries and combined with breeds established in the country to develop composite breed populations (Maijala, 1988; Fahmy, 1996). More than 250 papers have been published on Finnsheep and their crosses becoming one of the most studied breeds in the world (Fahmy, 1991). This is a unique example of a breed that could have been extinct had high fecundity not been considered as an economically important trait for commercial sheep production. Thus, the inherent potential of the Finnsheep has been conserved both as a purebred and composite breed population.

6. Evolution of composite goat breeds

In goats, the major effort has been towards grading-up to European dairy breeds based on the Saanen breed in Europe, Korea, Germany, Czech Republic and Russia, and the Toggenburg breed in Europe, Germany, Czech Republic and Russia (Quartermain, 1991). Similarly, the Angora breed that excels in Mohair production has been used for grading-up the Deccani and Gaddi breeds in India, and feral goats in Australia and

New Zealand. The productivity of upgraded goats has been adequate for specific objectives.

Grading-up by repeated crossing with the introduced breed is more popular in goats. This is in contrast to the development of composite breed populations in sheep. Nevertheless, 80 composite breed populations of goats have been developed in 37 countries (Table 2). Devendra (1991) has identified a number of goat breeds with potential to reach biological ceiling for the production of meat, milk, fiber and skin under varying agro-ecological zones. These breeds may be combined into composite breed populations to increase productivity. In the future, as breeds of goat with outstanding morphological characteristics and production performance are identified, composite breed populations with improved efficiency of production may be popular. This applies to those breeds that have some degree of risk and could reach critical levels but may be of value in the future with changes in the production system, environment and consumer preference for animal and animal products. Presently, there is the opportunity for the development of composite breed populations based on the Boer breed for the commercial production of meat from goat.

Table 2
Composite breed population of goats that have been developed in the world, number of foundation breeds and the year of origin or year recognized by country of origin

Country	Composite breed population	No. of foundation breeds[a]
Australia	Cashgora	2
Brazil	Branca sertaneja	2
	Parda sertaneja	2
	SRD	2
Bulgaria	Bulgarian White Dairy	2
China	Guanzhong Dairy	2 (1940)
	Hailun	3
	Hongtong	2
	Laoshan Dairy	2 (1919)
	Nanjiang Yellow	2 (1960)
Cyprus	Peratiki	2
Denmark	Danish Landrace	3
Fiji	Fiji	3
France	French Alpine	2 (1930)[b]
Germany	German Improved Fawn	2 (1928)[b]
	German Improved White	2 (1928)[b]
Hungary	Hungarian Improved	2^{+}
India	Indian Mohair	3 (1973)
	Malabari	2
	Ramdhan	2
Indonesia	Peranakan Etawah	2
Israel	Israeli Saanen	2 (1932)
	Yaez	2^{+}
Italy	Aquila	4
	Benevento	4
	Campobasso	4
	Ionica	2 (1981)[b]
	Potenza	3
Kazakhstan	Soviet Mohair	2 (1962)
Kenya	Kenya Dual-Purpose	4
Kyrgyzstan	Kirgiz	2
Mongolia	Gobi Wool goat	2
	Unjuul	2 (1982)
	Uuliin Bor	2 (1991)
Morocco	Fnideq	2
Mozambique	Pafuri	2 (1928)
The Netherlands	Dutch Pied	2
	Dutch Toggenburg	2
	Dutch White	2
Nigeria	Savanna Brown	2^{+}

7. Future considerations

Before forming composite populations, it is pertinent that optimal breeding objectives based on realistic economic values need to be defined. The genetic improvement of livestock and poultry species should include more than the size of genetic parameter estimates for what are considered economically important traits. For example, the biological, cultural, statistical, socio-economical and management aspects should be transparent in the decision making process. It is therefore important to assert that the composite populations based on endangered and established breeds are more suitable under varying agro-ecological zones found in most developing countries compared to the more popular breeds suitable for large commercial farms. This is because the high input associated with the outstanding productivity in those breeds is beyond the means of farmers with small holdings. Finally, in the future, advances in cloning of fertilized embryos based on stem cells, molecular markers related to production and resistance to diseases, and the precise modification of genetic information in the gametes based on genomics may provide new opportunities for the application of innovative technology in genetic resource conservation.

Table 2 (*Continued*)

Country	Composite breed population	No. of foundation breeds[a]
Norway	Norwegian	5
New Zealand	Kiko	2
Pakistan	Beiari	2
	Buchi	2
	Jattal	2
	Pak Angora	2
	Shurri	2
	Sind Desi	2
Romania	Banat White	3
Russia	Altai Mountain	2 (1982)
	Angora-Don	2
	Dagestan White	2
	Don-Kirgiz cross	2
	Russian White	2 (1905)
South Africa	Boer	2 (1959)[b]
Spain	Barreña	3
	Murcia-Granada	2 (1980)[b]
	Murcian	2 (1933)[b]
Tajikistan	Soviet Mohair	2 (1962)
Tanzania	Blended goat	3
Togo	Vogan	2
Turkey	Angora	2 (1900)[b]
	Bornova	3
	Çukurova	2
	Kilis	2
	Taurus	2 (1973)
Turkmen	Soviet Mohair	2 (1962)
United Kingdom	Anglo-Nubian	4 (1910)[b]
	British	3 (1896)[b]
	British Alpine	2 (1925)[b]
	British Cashmere	5
	British Saanen	2
	British Toggenburg	2
	English Guernsey	2^+
	Golden Guernsey	2^+ (1970)[b]
USA	Kinder	2 (1988)[b]
	Pygora	2 (1987)[b]
Uzbekistan	Soviet Mohair	2 (1962)
	Uzbek	2
	Uzbek Black	2 (1961)

Source: Mason (1996).

[a] Year of origin or year recognized.

[b] Year breeds society, association or stud book was established.

8. Conclusions

The application of existing scientific knowledge on quantitative genetic principles to the development of composite populations from a combination of endangered and established breeds can result in financial benefits from the superior productivity of the combination, and simultaneously the conservation of domestic animal diversity. Nevertheless, any segregating population without sufficient genetic variability to avoid inbreeding can have devastating consequences in the long term and must be avoided at all costs.

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