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1 Livestock Genetics and Breeding

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Executive Summary

Five challenges informed the historical choices of research priorities in livestock genetics and breeding at the International Livestock Research Institute (ILRI). The first challenge was to develop vaccines against two protozoan parasites causing African animal trypanosomiasis and theileriosis (East Coast fever), which led to novel work on cattle genetics. The second challenge, related to the first, was the need to understand trypanotolerance, the genetic ability of some animals to tolerate infection with the trypanosome parasite that causes trypanosomiasis in cattle. The third challenge, which came much later, was understanding the genetics of environmental adaptive attributes (especially diseases and climate challenges) in African livestock and their potential contribution to improving livestock productivity. The fourth challenge, on which ILRI's predecessor, the International Livestock Centre for Africa (ILCA), began work in 1992, was exploiting the potential of the genetic diversity of indigenous African livestock (ILCA, 1992). The fifth challenge was amassing research data on the comparative performance of breeds and genotypes (purebreds and cross-breds) in different production environments to inform cross-breeding programmes.

ILRI's contribution in the global context

The initial work of the International Laboratory for Research on Animal Diseases (ILRAD) concentrated on the genetic aspects of pathology and immunopathology of two major diseases of livestock: African animal trypanosomiasis and theileriosis. ILRI's characterization of animal genetic resources (AnGR), including work on diversity studies, trypanotolerance in cattle and endoparasite resistance in small ruminants, has since created unprecedented levels of awareness in national programmes of the uniqueness and potential of these genetic resources. The greater attention paid to indigenous livestock genetic resources led to more informed interventions to conserve and use these resources. The increased visibility resulted largely from research results, tools and methods by ILRI and its partners. The 'awakening' that ensued has enabled the national agricultural research systems (NARS) of Africa and Asia to play significant roles in expanding the characterization of their native livestock, and this has accelerated the coverage of many livestock populations across these continents.

While ILRI's substantive entry into designing on-farm breeding strategies is more recent, the progress already achieved has demonstrated promising possibilities for setting up working

models that can be used for data and informed breeding programmes leading to long-term genetic improvements within breeds and in cross-bred livestock populations.

According to altmetrics, by 2019, ILRI had contributed to 27% of the global research outputs on African livestock genetics and is a substantial contributor to the Scopus database on African animal genetics in general and on endoparasite resistance in particular. ILRI's classification of African cattle and small ruminant breeds remains a widely used standard reference. Some of the top-cited papers include: Clevers *et al.* (1990) on the bovine antigen structure (97th percentile in Scopus); Barendse *et al.* (1997) on the genetic linkage map of the bovine genome (97th percentile); Hanotte *et al.* (2002) on the genetic history and structure of African livestock (98th percentile); Hanotte *et al.* (2003) on mapping the quantitative trait loci (QTLs) controlling trypanotolerance in an N'Dama × Boran cross; Pain *et al.* (2005) on the comparative genetics of *T. annulata* and *T. parva* (97th percentile); and the Bovine HapMap Consortium (2009) on a genome-wide survey of variation in single-nucleotide polymorphisms (SNPs) and the genetic structure of cattle breeds.

Scientific impacts

ILRI's research findings on the genetics of disease resistance and genome mapping are widely recognized. The institute has made significant contributions to the discovery of candidate genes responsible for the phenotypic variation in livestock diseases and for phenotypic and genetic characterization of indigenous livestock using neutral markers. Together, these contributions have helped unravel the genetic history and geography of African livestock (cattle, sheep, goats, camelids and chickens), and have made significant contributions to our understanding of Asian livestock (yak, camelids, banteng, chickens, cattle, sheep and goats). Many publications of this research are highly cited globally, and the tools and methods are now used across Africa, Asia and other parts of the world.

Livestock genetics and breeding

ILRI delivered 'firsts' in many areas of livestock genetics and breeding. ILRI scientists identified molecular mechanisms and markers for defining trypanotolerant cattle types – polymorphisms that differentiate breeds such as the trypanotolerant N'Dama from non-trypanotolerant African Zebu types. They identified candidate chromosomal regions by mapping second-filial generation (F_2) N'Dama × Boran resource families, and subsequently candidate genes in pathways responding to infection with the causative parasite, *Trypanosoma congolense*, through genetic and expression analysis. This work examined variation in products of the major histocompatibility complex (MHC) loci, biochemical variants of a variety of gene products, and both mitochondrial and nuclear DNA polymorphisms. This work described a strategy for the discovery of candidate genes responsible for phenotypic variation in trypanotolerance, paving the way for subsequent expression analysis, *in vitro* testing of candidate pathways, genome mapping and population genetic work. Anticipating that identification of causative trypanotolerant genome mutations in cattle would come to light shortly, as such mutations had already been identified in wild species, ILRI led the cloning of the first African indigenous transgenic livestock by somatic cell nuclear transfer using primary embryonic fibroblasts. Tumaini (Kiswahili for 'hope') is the result – a Kenyan Boran bull born on ILRI's research facility in Nairobi. This cloning success has opened up the possibility of genetically engineering African livestock using foreign genes for desired traits (such as disease resistance) through genome editing at the fibroblast level followed by somatic cell nuclear transfer.

Genetic characterization and history of livestock

ILRI delivered the first comprehensive classification of African cattle breed and strain groups, including the status of their risk of extinction, and the first and most compelling reconstruction of the genetic history of indigenous African cattle. One of the papers (Hanotte *et al.*, 2002), published in *Science*, won a CGIAR Science Award as 'Outstanding Scientific Article' in 2003 and remains a key reference on the genetic history of African cattle, ranking in the 98th percentile in Scopus citations in its field to March 2020. Similarly, ILRI described the first complete molecular characterization of Mongolian and Russian yak populations, supporting their

distinct genetic entities for conservation and breeding programmes, including the first molecular validation of cattle introgression into the yak genome. Using these novel approaches, ILRI scientists and collaborators made the first report of multiple introduction routes of chicken on the African continent (terrestrial and maritime) and documentation of a directional gene flow from domestic chickens into free-ranging wild red junglefowl. Similarly, ILRI and its collaborators developed a comprehensive genetic history of African sheep and classified Ethiopian sheep breeds. ILRI also validated the first set of molecular markers for the genetic characterization of camelids and undertook the first molecular characterization and classification of Kenyan dromedary breeds. These are now papers of reference for the history of the dromedary, revealing the dynamics of their domestication and cross-continental dispersal. Similarly pioneering was the finding of Ethiopia as one of the centres of genetic diversity (and potentially of domestication) for domestic donkeys in the Horn of Africa.

Breeding technologies

Of direct relevance to millions of farmers across Africa (and Asia), ILRI made the first application of SNP technology to identify genotypes *in situ* in smallholder systems (disclosing what genotypes farmers currently have) and to estimate genotype differences among a diverse range of genotypes kept by these farmers. ILRI has also demonstrated the feasibility of making genetic improvements through within-breed selection in village poultry systems.

Development impacts

Much of ILRI's work has had policy and development impacts in animal genetics and breeding. Elucidation of the genetic uniqueness of indigenous livestock and the special adaptive attributes of certain breeds have provided critical evidence of the potential of indigenous livestock, which has catalysed actions for their conservation and use in Africa and Asia. In the absence of breed-level livestock census data, breed survey tools developed by ILRI are being applied by countries to estimate populations and trends in individual indigenous breeds. More recently, an innovation platform of the Dairy Genetics East Africa (DGEA) project helped identify business opportunities in the dairy value chain (heifer production, semen production and field delivery), which are now operational. The DGEA project provided compelling evidence that innovative application of genomic and associated technologies can be transformative.

ILRI has made global contributions to the development of economic valuation tools to inform the prioritization of breeds and resource allocations for conservation programmes and the Global Strategy on Animal Genetic Resources for Food and Agriculture led by the Food and Agriculture Organization of the United Nations (FAO). ILRI also established and continues to maintain the Domestic Animal Genetic Resources Information System (DAGRIS) as a research and development tool providing access to much-needed information and data for researchers and development practitioners.

Capacity development

ILRI has built significant capacity in livestock genetics and breeding through its master's and doctoral trainings as well as through its mentorship of practising scientists in collaborative projects and group training courses. While livestock genetics and breeding research remain comparatively weak throughout Africa, ILRI's capacity strengthening efforts, made through graduate training, secondments, group training and advisory services, have created a cadre of high-level experts in African countries who are generating new outputs in livestock genetics and breeding.

ILRI has supported at least 200 Bachelor of Science students, 70 Master of Science students, 65 doctoral students, 35 visiting scientists and postdoctoral fellows, and 150 short-term trainees in genetics, breeding and related fields. Many of the beneficiaries of these capacity strengthening efforts are driving the livestock genetics research agenda across the sub-Saharan continent, with some now internationally recognized experts in their own right.

Partnerships

Partnerships with national programmes have been the basis of nearly all research at ILRI.

Other than the resource populations used in genetics of disease resistance – the N'Dama cattle herd, the Red Maasai and Dorper sheep flocks, the Galla and Small East African goat flocks, and the mouse lines in ILRI's laboratories – all of ILRI's genetics and breeding research was based on animals owned by NARS institutions or farmer-owned animals accessed through NARS collaboration. ILCA and ILRAD worked closely with the International Trypanotolerance Centre (ITC) in The Gambia and the Centre International de Recherche-Développement sur l'Elevage en zone Sub-humide (CIRDES/ILRI/ITC, 2000) in Burkina Faso. ILRI's work has also benefitted from collaboration with universities and national programmes in the Global North (Europe, North America and Australia), in Asia (China and Korea), and in Latin America (Brazil). FAO has been a critical partner of ILRI, especially through engagement of ILRI experts in formulating the Global Plan of Action for Animal Genetic Resources, for example, by contributing to the development of tools, protocols and guidelines for characterizations across the globe.

Introduction

Scientific understanding of African and Asian livestock has improved remarkably since ILRAD and ILCA were established in 1973–1974. At that time, countries classified livestock by species with limited reference to breeds, strains or types (Payne, 1970). The only widely applied within-species distinction was that made among indigenous types, exotics and crosses between the two. Exotic animals were uniquely and consistently identified as distinct breeds and further classified into output- or commodity-specific types – dairy, meat or wool – reflecting the fact that long-term within-breed genetic improvement had successfully produced these specialized European breeds.

While the works of Epstein (1971) and Mason (1988) on classification of African livestock were cited, indigenous livestock continued to be lumped together as though they were a uniform genetic group. Impressionistic accounts of indigenous 'breeds' suggested – indeed, emphasized – that their productivity was low compared with European livestock. The indigenous animals were generally considered less worthy of attention than the exotics, and many efforts were made to 'upgrade' them, the vision then being that they would gradually transition into 'grade livestock' and eventually into pure exotic types. This was widely considered to be the main strategy for improving livestock productivity in Africa and Asia. From the 1950s and 1960s through to the late 1970s, the word shenzi, which is Kiswahili for uncivilized, uncultured, uncouth or even filthy, and its equivalents in other parts of Africa were commonly used in reference to indigenous livestock.

At the species level, national livestock statistics continued to be presented at the level of native or indigenous versus exotics and crosses. While some results across the continent showed that the productivity of local types could be improved under better management, the baseline was still so limited that the importation of exotic breeds was seen as the means to breed more productive livestock (Blench, 1997). The few successful European settler farms using European breeds, although usually based on economically unrealistic management practices (Dunbar, 1970), seemed to validate such a strategy.

Endowed with more resources than was previously available for livestock research and development on the continent and guided by more forward-looking research agendas informed by stakeholder consultations, ILCA and ILRAD were able to put together well-trained teams and agricultural research and development programmes with the ability to mobilize and apply available and emerging scientific tools. ILCA and ILRAD programme priorities in their early days, from the 1970s and to the early 1980s, had one thing in common: a focus on understanding context. In relation to genetics and livestock improvement, ILCA's entry point was understanding the performance of different livestock genotypes (indigenous, exotics and crosses) in different production systems. ILRAD's focus in this domain was more specific: confirming indigenous breeds that were reported to be able to survive and produce under trypanosomiasis challenge (i.e. possessing the trypanotolerance trait). These initial priorities developed over time into major programme initiatives over three decades – the AnGR programme, which included molecular genetic characterization, and the genetics of disease resistance programme, focusing on trypanosomiasis and endoparasites.

While not 'complete' by any measure, much more is known today about indigenous livestock in developing countries; many breeds and strains have now been identified with specific attributes and some anecdotal claims are now supported with data.

ILRI has contributed significantly to documenting diversity among populations within species, providing evidence to match genotypes to environments, and unravelling the genetics underpinning observed differences, including in adaptive attributes anecdotally referenced in earlier reports. In major ways, ILRI research has provided the evidence now used widely in 'calls for action' for the conservation of the unique genetic diversity found in indigenous livestock, and these results are now informing conservation strategies.

Genetic improvement of indigenous livestock

The rate of progress made in *understanding* indigenous livestock – and the role that ILRI has played in this – is much greater than that in the genetic *improvement* of livestock in Africa (and Asia). There are at least two major and interrelated reasons why genetic improvement of local African and Asian breeds has received comparatively little attention: (i) the decades-long perception that these breeds are inferior to exotic breeds; and (ii) the original (and persisting) belief that cross-breeding is an effective and sustainable shortcut to productivity improvement, with inadequate considerations given to the important role of indigenous livestock adaptations to their environments. This continues to be the case, even after studies have shown that time and capital invested in selection within local breeds can, and does, eventually lead to adapted and profitable populations (FAO, 2013). Even where attempts have been made in recent decades to pay attention to local breeds, informed by the results of genotype characterization, the primary focus of such initiatives has been to conserve and use local animals as they are, with very little investment in selective breeding.

The few attempts made to genetically improve indigenous breeds through various nucleus breeding schemes (and other approaches) have tended to be short-term atomized projects with no opportunity to demonstrate tangible genetic progress. The end result is that local breeds have remained uncompetitive, especially because the metrics used for comparisons have focused on productivity as measured in terms of quantities of milk, meat, eggs, growth rate, etc., with little reference to the economics of production under different production constraints, such as disease, poor feeds and excessive heat. The lack of performance and pedigree recording in developing countries, which has been a major driver of the success of breeding programmes in the Global North, has compounded the problem. In the absence of robust recording systems, the 'eye-balling' and memory approach used in traditional livestock systems does not have the same discriminatory power to deliver the required selection differentials and accuracies, especially in view of the large environmental noise that is typical in smallholder systems. Continued inferior economic performance of local breeds reduces farmers' interest in those breeds, and they become threatened with extinction (Rege, 2008).

At the time of ILRI's founding, two mutually reinforcing actions were needed in developing-country situations: (i) to increase the economic performance of indigenous animals, with more output and/or less cost; and (ii) to conserve livestock breeds not yet supported by market forces. While the early work of ILRI provided useful information on genotype comparisons under different production environments, ILRI's direct and explicit entry into the area of livestock genetic improvement is more recent (starting in 2000). This work is taking advantage of recent developments in the areas of genomics and information and communication technologies to speed up the pace of genetic improvements in, and for, smallholder livestock systems.

This chapter summarizes ILRI's work in livestock genetics and breeding, with a focus on scientific and development impacts since the establishment of ILCA and ILRAD. The chapter is organized in the following sections: (i) characterization of livestock genetic resources; (ii) genetics of disease resistance/tolerance, focusing on trypanotolerance in cattle and endoparasites in small ruminants; (iii) genetic improvement strategies; and (iv) strengthening the capacity of NARS to conduct and use this work. Figure 1.1

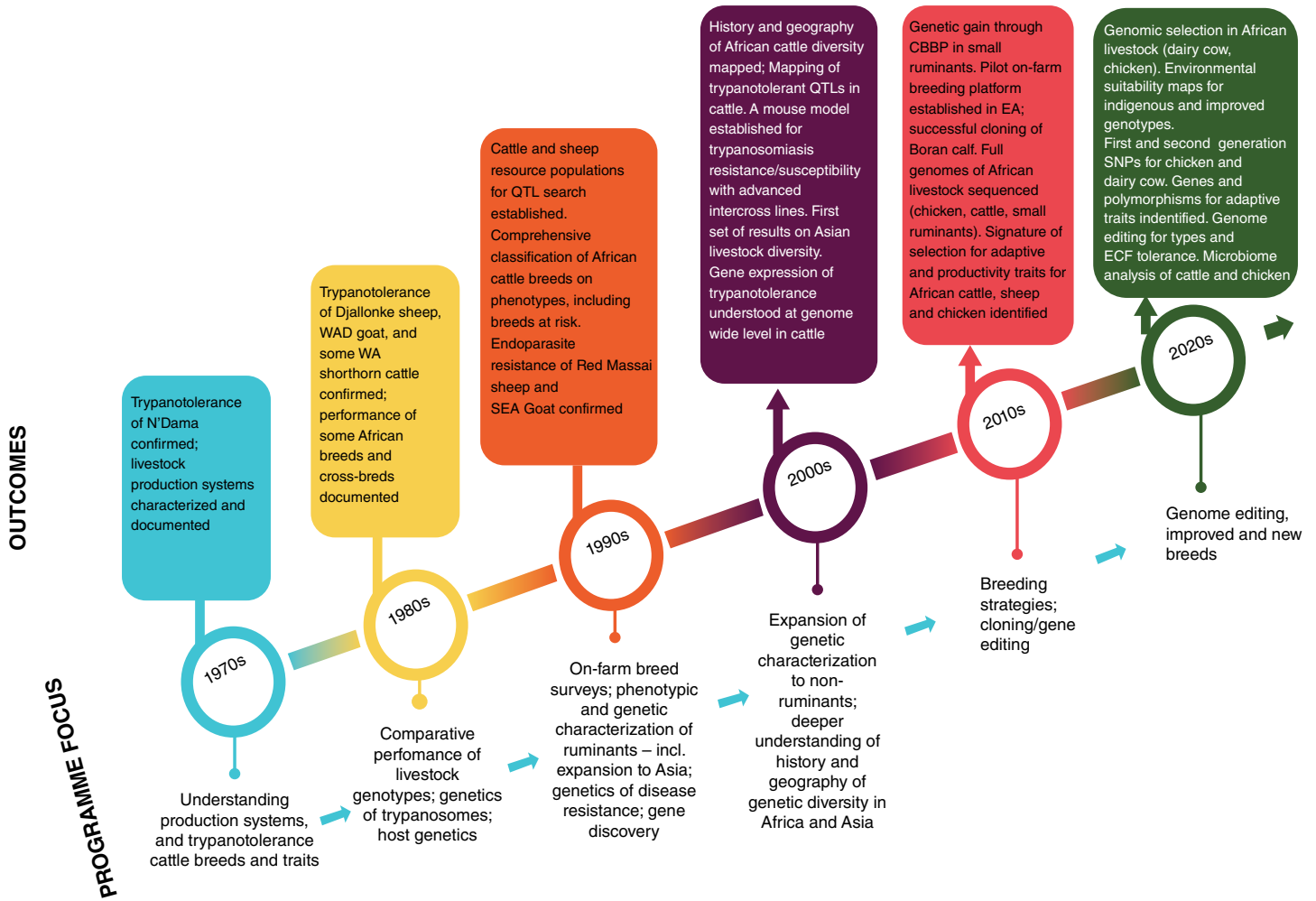

Fig. 1.1. Evolution of the ILRI genetics portfolio, 1970s to 2020. EA, East Africa; ECF, East Coast fever; CBBP, community-based breeding programme; SEA, Small East African; WA, West African; WAD, West African Dwarf.

summarizes the past and present outcomes and impacts of ILRI's genetics programme portfolio since the mid-1970s and ILRI's projected future focus in this area.

Characterization of Animal Genetic Resources

The developing regions of Africa and Asia have rich reservoirs of AnGR. Until the 1990s, information on the genetic diversity of this reservoir was lacking, limiting development of livestock conservation and use strategies. Characterization of AnGR – the distillation of all available knowledge, both published and unpublished, that contributes to the reliable prediction of genetic performance in defined environments – includes measurable/observable performance as well as the underlying genetic diversity, whether related to the observable performance or not. Work to characterize AnGR includes defining both the genetic attributes of a population possessing a unique genetic identity and the environment to which it is adapted or known to be partially adapted (Rege, 1992). While breed evaluation and comparison (based on phenotypic information) is an important aspect of characterization that provides information on performance (including adaptation), genetic characterization refers to the description of attributes that involve specific DNA sequences. The conservation of AnGR entails actions designed to prevent loss of the genetic distinctiveness of different species, subspecies, breeds or populations due to concerns that existing phenotypes, genetic integrity and local adaptations need to be maintained. It is, however, increasingly recognized that in the face of environmental change the conservation of adaptability and the processes sustaining and providing diversity might be of greater general importance than a focus only on conserving specific local adaptations. Knowledge, including local indigenous knowledge, of population differentiations and the temporal and spatial extent of gene flows is therefore essential to management decision making. This section highlights both direct and indirect ILRI contributions to the characterization of African and Asian AnGR over the past four decades.

Phenotypic characterization and breed surveys

Early work in phenotypic characterization of indigenous breeds and their crosses with exotic types formed the foundation of what later evolved to become animal genetics and breeding at ILRI. This work initially focused predominantly on production traits – growth, milk yield and reproductive traits. The only substantive work on adaptive traits (in the broad sense) in the 1980s was the work on trypanotolerance – the ability of some livestock breeds and strains to survive and produce under trypanosomiasis challenge (Trail *et al.*, 1979b; ILCA, 1979; see Chapters 2 and 3, this volume). Trypanotolerance was important due to the high livestock productivity losses associated with trypanosomiasis. These huge losses effectively curtail the use of livestock across vast regions of Africa that are infested by the tsetse fly, which transmits the disease-causing trypanosome parasites to the animals when the flies take a blood meal. The first continent-wide effort to characterize African AnGR was spearheaded by ILCA starting in 1992 (Rege and Lipner, 1992), and this set the stage for continental AnGR characterization efforts, eventually covering all the major livestock species of Africa and later expanding into Asia. The initial phase of this research was aimed at developing, in collaboration with NARS and FAO, baseline information on Africa's livestock – the number of breeds, sizes of populations, their indicative performance and their typical traditional production environments.

Tools and methods for conducting breed surveys

Previously, a major limitation to the phenotypic characterization mission was the lack of methods for conducting breed surveys and phenotypic characterization. In collaboration with FAO and other partners, ILRI scientists made a major contribution to this initiative by developing new instruments for breed surveys. They developed random cluster and transect survey methods for estimating herd/flock structures and partitioning species-level population statistics into breed-level census data for use in determining the risk status of ruminant breeds. They also published breed survey guidelines

(Rowlands *et al.*, 2003; Ayalew *et al.*, 2004) for use throughout Africa and Asia.

Classification of African livestock populations

Another notable contribution by ILRI and partners has been the comprehensive classification of African livestock populations through breed surveys and phenotypic characterization. ILRI spearheaded the first continent-wide initiative to characterize African AnGR starting in 1992 (Rege and Lipner, 1992). ILCA's systematic breed surveys led to the first comprehensive classification of African cattle (Rege *et al.*, 1994a,b,c; Aboagye *et al.*, 1994; Rege, 1999a). This set the stage for what were to become major continental AnGR characterization efforts. These efforts involved many international and national stakeholders and linked with a global plan under development by FAO 'to preserve the ancestral gene pool of domestic animals in the developing world'. This work built on breed evaluation activities that ILCA was already undertaking in collaboration with NARS under a Cattle and Small Ruminant Thrusts initiative and expanded the scope to encompass breed surveys focusing on identification, quantitative and qualitative description of breeds and the natural habitats and production systems to which they were adapted.

The first efforts focused on cattle. The first major description of African domestic cattle had been prepared by Doutressoulle (1947), while Epstein (1971) carried out the most comprehensive review of the era before ILRAD. Attempts had previously been made to construct outlines with the aid of archaeological (Epstein and Mason, 1984; Muzzolini, 1983; Clutton-Brock, 1989) and other (Blench, 1993; Doutressoulle, 1947; Epstein, 1971) evidence.

The first papers (Trail *et al.*, 1979a,b; Shaw and Hoste, 1987) surveyed the distribution of trypanotolerant cattle of West and Central Africa. Subsequent efforts by Rege *et al.* (1994a,b,c), Aboagye *et al.* (1994), Rege (1999b) and Rege and Tawah (1999) represented the most systematic classifications of African cattle and cattle populations, and included production systems, characteristics and extinction risk. This continental survey confirmed that phenotypically humped cattle – the 'non-native' Zebu cattle of Africa – constituted the majority of African cattle. Subsequent molecular work demonstrated that African Zebu cattle are ancient hybrids of African *Bos taurus* with *Bos indicus* of historical Asian origin. Contemporary African cattle populations were assigned to four broad categories: the humpless *B. taurus*; the humped African Zebu, distributed widely in Africa; *B. taurus* × *B. indicus* derivatives (sanga), found mainly in eastern and southern Africa; and sanga × Zebu types (termed the 'zenga'), such as the Fogera and Horro of Ethiopia and the Nganda of Uganda. The taurine (humpless) type has two subgroups – longhorns (*B. taurus longifrons*) and shorthorns (*B. taurus brachyceros*) – both of which were (and still are) restricted to West and Central Africa. While the longhorns are represented by two breeds only – the N'Dama and the Kuri – the shorthorn subgroup has numerous representatives (Box 1.1). The survey revealed that sub-Saharan Africa is home to a total of at least 145 cattle breeds/strains comprising two taurine longhorns, 15 taurine shorthorns, 75 Zebu (*B. indicus*), 30 sanga, eight zenga, nine 'recent' breeds derived from interbreeding of indigenous breeds/strains located in close proximity to each other and six systematically created composite breeds. Of the 145 breeds identified from these studies, using the FAO's classification, 47 (about 32%) were considered to be at risk of extinction. Of the breeds identified as at risk of extinction, six were in the 'rare' category, ten were 'vulnerable', another ten were 'endangered' and 15 were 'critical'. A total of 22 breeds previously recognized on the continent were determined to have become extinct in the past century. This number excluded some populations that were considered to have lost individual identities due to admixtures involving two or more originally distinct breeds.

The European (commercial) taurine breeds and their cross-breds were also found in many parts of the continent, but their populations then, as today, were relatively low compared with the indigenous breeds. Taking a cue from these surveys, NARS scientists in many countries, working independently or in collaboration with ILRI, started to undertake similar on-farm surveys and detailed studies of individual breeds. Examples include Mekonnen *et al.* (2012) working on Horro cattle; Tawah and Rege (1996a,b) on Gudali and white Fulani cattle; Tawah *et al.* (1997) on Kuri cattle; and Rege *et al.* (2001),

Box 1.1. The taurine cattle of West Africa.

The review of West African taurine breeds sought to determine the extent to which those breeds are endangered and to inform conservation decisions. The reviews addressed origin, distribution, population statistics, habitat, management and production systems, description, adaptability, disease resistance and performance characteristics.

West African taurine cattle breeds include the hamitic longhorns (*Bos taurus longifrons*) and the shorthorns (*Bos taurus brachyceros*). Only two longhorn breeds are found in West Africa – the N'Dama and the Kuri. The shorthorn population is much more varied and their breeds/strains are known by a variety of names, depending largely on their location, including Muturu (Liberia and Nigeria), Lagune (Benin, Côte d'Ivoire and Togo), Ghana shorthorn, Baoulé (Burkina Faso and Côte d'Ivoire), Somba (Benin and Togo), Bakosi, Bakweri, Doayo and Kapsiki (Cameroon), Lobi (Burkina Faso and Côte d'Ivoire), Manjaca (Guinea Bissau) and Logone (Chad). However, it is not clear whether all of these populations are different enough to deserve different names (this classification challenge pointed to the need for genetic diversity studies, which were to follow). With the possible exception of Kuri cattle, which live in a special environment where tsetse flies have not been recorded, these breeds have developed in tsetse-infested areas and are thought to have developed various degrees of trypanotolerance. The N'Dama is the best known, most numerous and most widely spread of the trypanotolerant breeds, with a total of nearly 5 million head spread throughout West and Central Africa. However, the population of all West African shorthorns is only around 2 million head, and several breeds, including the Muturu and Lagune, are at risk of extinction, mainly due to cross-breeding (especially with Zebus), to neglect and to reduction of pastoral lands as human population pressure increases.

Mwacharo and Rege (2002) and Mwacharo *et al.* (2006a) on East African Zebu. A clear pattern of the different phenotypic characteristics and distribution of different types of African cattle populations emerged from these studies.

Breed characterization soon thereafter became a major area of livestock research. Most of these initiatives were conducted by ILRI in collaboration with NARS (Rege and Lebbie, 2000), or were inspired or directly influenced by the work of ILRI. The work expanded to sheep and goats (Farm Africa/ILRI, 1996; Warui, 2008; Abegaz *et al.*, 2013; Taye *et al.*, 2016) and thereafter to chickens (Halima *et al.*, 2007; Dana *et al.*, 2010; Dessie *et al.*, 2012) and camels (Ishag *et al.*, 2010; Tandoh *et al.*, 2018).

Molecular genetic characterization

When ILRAD and ILCA merged in 1995, the ILCA Animal Genetic Resources programme and the ILRAD Genetics of Disease Resistance programme were already organizing a global programme on molecular genetic diversity of livestock. The large phenotypic variation observed among African populations of cattle, sheep and goats was used to formulate the hypotheses that formed the basis of the genetic diversity studies. As was the case with phenotypic characterization, the first major set of ILRI-led molecular diversity studies started with African cattle. A concerted effort was initiated in 1995 to collect biological samples for DNA extraction for this purpose. Coinciding with the emergence and increasing application of a wide range of genetic markers, these studies attracted many scientists to the power of 'neutral' molecular markers in unravelling genetic structure and estimating diversity in livestock populations.

By 1993, scientists had developed and tested a panel of short sequence repeat markers and methods for global use in genetic diversity studies of different livestock species (Brezinsky *et al.*, 1993a,b,c; Kemp *et al.*, 1992, 1995). As such, ILRI was a major contributor from the start to the FAO-coordinated 'Molecular Domestic Animal Diversity' – which identified and published panels of markers to be used globally for genetic diversity studies of different livestock species (FAO, 1993) – and to the secondary guidelines developed (ISAG/FAO, 2004); the FAO marker panel included many of those developed and tested by ILRI. These markers and methodologies catalysed significant investments in AnGR characterization in Africa using a variety of markers. The co-development of the 30-microsatellite marker panel, related capacity development efforts, and the wider domestication and use of these methods has led to accelerated and high-quality characterization of a large number of indigenous livestock breeds in Africa and Asia. This has

consequently led to increased understanding of genetic diversity and thus informed conservation efforts, including regional gene banks, Sheko semen banks in Ethiopia, Ankole semen banks in Uganda and local/indigenous chicken germ-cell banks in ILRI Kenya, among other efforts.

First genetic history of cattle in Africa, linking livestock to human history

Utilizing the tools and methods developed, ILRI scientists established the genetic relationship of more than 31 breeds of African and Asian cattle and reconstructed the first genetic history of cattle in Africa (Hanotte *et al.*, 2002), linking livestock to human history and providing a glimpse into the distant past of the peoples and civilizations of Africa and Asia. The major cumulative result of this work has been the knowledge base of the history and geography of the genetic diversity of domestic livestock of Africa and Asia.

Taken together, these studies led to the conclusion that the earliest cattle of Africa were of taurine *B. taurus* type. Subsequent waves of migrations of humped Zebu (*B. indicus*) animals then reshaped the genomic landscape of African cattle (Bradley *et al.*, 1994; Hanotte *et al.*, 2002; Freeman *et al.*, 2004). African and European cattle seem to be more closely related and quite distinct from Indian cattle, the relatively large divergence providing evidence for two separate domestication events, presumably of different subspecies of the aurochs, *Bos primigenius* (Loftus *et al.*, 1994). Today, the African continent is uniquely rich in cattle diversity, with an estimated 145–150 African cattle breeds or populations recognized (Rege, 1999b; Mwai *et al.*, 2015). Importantly, it is now well established that African cattle carry a taurine maternal ancestry originating from the Near East taurine domestication centre(s), while the possible genetic contribution of the now-extinct African auroch (*B. primigenius opisthonomous*) remains unclear (Epstein, 1971; Bonfiglio *et al.*, 2012; Decker *et al.*, 2014). The pattern of introgression of the Zebu genome across the southern, eastern and north-western parts of sub-Saharan Africa has been well documented using autosomal and Y-chromosome-specific microsatellite loci (Bradley *et al.*, 1994; Hanotte *et al.*, 2000a; Freeman *et al.*, 2004).

African cattle inhabit more than five distinct major agroecological zones. Overall, Zebu cattle are common in the arid and semi-arid northern Sahelo-Sudanian zone, as well as in the eastern part of the continent, including the highlands, whereas taurine cattle today form the majority of the herds in the subhumid and humid regions of West Africa, which are heavily infested with tsetse fly. Sanga are predominant in the western region of Central Africa, around the Great Lakes region, and in the southern part of the continent. The highest genetic diversity is among African Zebu and sanga cattle (Kim *et al.*, 2017). No pure indigenous *B. indicus* cattle occur on the African continent. These findings have informed strategies for genetic characterization and have direct and important implications for AnGR conservation and use, as they point to population location phenotypes and uniqueness.

Genetic history and geography of African sheep

Indigenous African sheep genetic resources have been classified into two main groups, fat-tailed and thin-tailed sheep. The fat-tailed sheep are the most widely distributed, being found in a large part of North Africa (from Egypt to Algeria) and in eastern and southern Africa (from Eritrea to South Africa). The thin-tailed sheep are present mainly in Morocco, Sudan and West Africa. Historically, African sheep were domesticated outside of Africa. They share a common ancestry with European and Asian sheep. Archaeological information supports separate introductions and dispersion histories for the African thin-tailed and fat-tailed sheep. The first sheep entered Africa via the Isthmus of Suez and/or the southern Sinai Peninsula between 7500 and 7000 BP. They were likely of the thin-tailed type. Fat-tailed sheep entered Africa through its north-eastern part and the Horn of Africa. Mitochondrial DNA analysis supports a common maternal ancestral origin for all African sheep, while autosomal and Y-chromosome DNA analysis indicates a distinct genetic history for African thin-tailed and fat-tailed sheep, and the main ancestral population of southern African fat-tailed sheep probably originated in East Africa (Muigai and Hanotte, 2013).

Genetic history and geography of African chickens

ILRI has made a major contribution to the body of knowledge of African chicken origin and present-day diversity (e.g. Lyimo *et al.*, 2014). Sociocultural, linguistic, archaeological and historical data together suggest a complex history of present-day African chicken populations. Introductions evidently occurred via land and sea routes followed by several subsequent dispersal routes across the continent (Mwacharo *et al.*, 2013b). Molecular genetic studies support the origin and migration models for African domestic chickens and suggest centres of origin in Asia, including South Asia and South-east Asia. Studies have consistently found that indigenous chickens are uniquely adapted to their local agroecologies and are distinct from commercial broiler and egg layer lines (Bettridge *et al.*, 2018). More localized studies have been used to test specific hypothesis on origins. For example, results of a study reported evidence for a dual geographical and genetic origin for the indigenous Malagasy chickens, specifically, their relationship to Asian breeds and, more particularly, to Indonesian chickens (Razafindraibe *et al.*, 2008). However, a subsequent in-depth study (Herrera *et al.*, 2017) has reported findings suggesting a much stronger relationship between Malagasy and East African chicken populations, putting an interesting spin on the earlier link of the genetic origin due to an important functional genetic trait – susceptibility/resistance to viral (avian influenza) infection (Razafindraibe *et al.*, 2008). Using autosomal microsatellite markers, Mwacharo *et al.* (2013b) identified three distinct autosomal gene pools (I–III) in eastern African chicken populations, possibly representing genetic signatures of separate events in the history of the continent that relate to the arrival and dispersal of village chickens and humans across the region. Earlier, analysis of mitochondrial DNA indicated a probable Indian subcontinent origin for the commonest haplogroup and a maritime introduction for the next commonest one from South-east and/or East Asia (Mwacharo *et al.*, 2011). These findings not only support ancient historical maritime and terrestrial contacts between Asia and East Africa but also indicate the presence of large maternal genetic diversity in the region, which could support genetic improvement programmes. It is anticipated that further continent-wide studies combining archaeological, ancient and/or modern genetic information are likely to shed new insights on the history of chickens in Africa, as well as globally.

Genetic history and geography of the African dromedary

The dromedary has a higher initial diversity relative to the native distribution of its wild ancestor on the Arabian Peninsula and to the brief coexistence of early-domesticated and wild individuals compared with other livestock, which show a long history of gene flow with their wild ancestors. Mburu *et al.* (2003) reported results not supporting the classification of the indigenous Kenyan dromedary into four distinct breeds based on socio-geographical criteria; instead, their results pointed to only two separate genetic entities, the Somali population on the one hand and a group including the Gabbra, Rendille and Turkana populations on the other. Extending this work to Africa and Asia, phylogenetic analyses of ancient and modern dromedaries suggest a history of restocking from wild relatives from the south-east coast of the Arabian Peninsula following domestication (Almathen *et al.*, 2016). The results suggested that the classic models of domestication from multiple centres and from wild conspecific individuals in isolation may not be applicable to the dromedary. Molecular genetic analyses have revealed a relative lack of genetic differentiation among dromedaries living in different areas; this is a possible legacy of ancient trading routes converging at Mediterranean ports where goods, including the packing animals carrying them, were exchanged (Almathen *et al.*, 2016).

Establishment of a joint laboratory with CAAS in Beijing and expansion into Asia

Understanding the genetic diversity of domestic stock requires attention to Asia both because of the importance of Asia in the history of many African livestock populations and because of Asia's endowment with livestock genetic diversity. Thus, ILRI's early sampling strategies for genetic diversity studies included coverage of strategic areas in Asia and included more than

just reference populations for African livestock species; the coverage included species not farmed in Africa, such as water buffalo, yak, banteng and Bactrian camels. Work in Asia was significantly strengthened when, starting in 2005, ILRI established a joint laboratory in Beijing with the Chinese Academy of Agricultural Sciences (CAAS) to support livestock and forage genetic resources work. Subsequent funding enhanced the quality of science and capacity in AnGR for Bangladesh, Sri Lanka and Vietnam, among other countries, allowing the wider application of FAO's panel of genetic markers. The ILRI-CAAS Joint Laboratory significantly increased ILRI's presence in, and impact on, the Asian continent. Although quantitative estimates were variable, the results across all species began to draw attention to the uniqueness of various local populations or 'breeds' not just in Africa but also across Asia, such as yak (Jianlin *et al.*, 2002; Xuebin *et al.*, 2005; Qi *et al.*, 2010), camelids (Jianlin *et al.*, 2000, 2004); banteng (Nijman *et al.*, 2003) and cattle (Dorji *et al.*, 2003). Going beyond its intended role, the joint laboratory and its associated capacity working with other laboratories enabled China, in 2018 during the African swine fever outbreak, to put in place polymerase chain reaction (PCR)-based diagnostics to support disease surveillance. Specifically, sequencing analysis of a 417 bp region of the *B646L/p72* gene of the virus helped trace the outbreak to the Georgian strain of the virus in Russia and Eastern Europe (Wang *et al.*, 2018).

ILRI's genetic characterization as a catalyst for international interest

ILRI's efforts in molecular characterization catalysed significant investments in this area, while beginning to provide genetic links to populations of other regions using a variety of markers to study subsets of populations, ranging from single countries to groups of countries in a subregion of the continent to the whole continent. Indeed, as part of ILRI's entry into Asia, its genetics programme activities were among the first to move ILRI's work into Asia and to strengthen its work on cattle (Okomo *et al.*, 1998; Hanotte *et al.*, 2000b; Hanotte *et al.*, 2002; Hassen *et al.*, 2007; Ndumu *et al.*, 2008; Kugonza *et al.*, 2011; Kim *et al.*, 2017; Taye *et al.*, 2018), sheep (Gizaw *et al.*, 2007; Muigai *et al.*, 2009; Muigai and Hanotte, 2013), goats (Chenyambuga *et al.*, 2004; Tarekegn *et al.*, 2018), chickens (Mwacharo *et al.*, 2007; Razafindraibe *et al.*, 2008; Mwacharo *et al.*, 2011; Dessie *et al.*, 2012; Wragg *et al.*, 2012; Desta *et al.*, 2013; Mwacharo *et al.*, 2013a,b; Bettridge *et al.*, 2018; Park *et al.*, 2018) and camelids (Jianlin *et al.*, 2000; Mburu *et al.*, 2003; Jianlin *et al.*, 2004; Almathen *et al.*, 2016), applying a range of markers, starting with the first-generation DNA markers (restriction fragment length polymorphisms, minisatellites, microsatellites and mitochondrial DNA).

Demonstrating the unique attributes of indigenous livestock has provided a strong rationale for conservation and use of indigenous animals. Other scientific outcomes included improving the body of knowledge of the origin and diversity of African cattle (Hanotte *et al.*, 2002), sheep (Muigai and Hanotte, 2013) and chicken (Mwacharo *et al.*, 2006b; Mwacharo *et al.*, 2013a), grossly expanding the knowledge base of the history and geography of the genetic diversity of the domestic livestock of Africa and Asia. These 'pathfinder' studies triggered subsequent studies (Decker *et al.*, 2014), which analysed an expanded cattle data set worldwide (134 breeds), showing ancient African cattle to have been first domesticated in the Fertile Crescent of the Middle East and then brought to Africa by migrating peoples thousands of years ago. Today, the study of the genetic diversity of livestock at the molecular level has developed into an active area of research, with African results receiving considerable new attention by the scientific community.

ILRI's genetics and breeding work on African cattle included many 'firsts', such as comprehensive classification of breed/strain groups, including their status of risk of extinction (Rege *et al.*, 1994a,b,c) and reconstruction of their genetic history (Hanotte *et al.*, 2002). Other 'firsts' included: the complete molecular characterization of Mongolian and Russian yak populations, supporting their distinct genetic entities for conservation and breeding programmes (Xuebin *et al.*, 2005); molecular validation of cattle introgression into the yak genome (Jianlin *et al.*, 2002; Qi *et al.*, 2010); reports of multiple introduction routes of chicken on to the African continent (terrestrial and maritime) (Mwacharo

et al., 2013a,b); a comprehensive genetic history of African sheep (Muigai and Hanotte, 2013) and a classification of Ethiopian sheep breeds (Gizaw *et al.*, 2007); documentation of a directional gene flow from domestic chickens into free-ranging wild red junglefowl, calling attention to interpretation of genetic data applied to a genetic approach to the conservation of the red junglefowl (Thakur *et al.*, 2018); the molecular characterization of the dromedary, which reclassified the four traditional Kenyan dromedary breeds (Somali, Turkana, Rendille and Gabbra) into two genetic entities, the Somali and a second group comprising the Gabbra, Rendille and Turkana populations (Mburu *et al.*, 2003); validation of the first set of molecular markers for the genetic characterization of camelids (Jianlin *et al.*, 2000); the paper of reference for the history of the dromedary, revealing the dynamics of domestication and the cross-continental dispersal of the dromedary (Almathen *et al.*, 2016); and the finding of Ethiopia as one of the centres of genetic diversity (and potentially domestication) for domestic donkeys in the Horn of Africa (Kefena *et al.*, 2014).

Genetics of Disease Resistance

Genetics of trypanotolerance

The earliest major collaboration between ILRAD and ILCA was field characterization of trypanotolerant livestock – breeds reported to be able to survive and produce under trypanosomiasis challenge – in Africa. The African Trypanotolerant Livestock Network (ATLN) of NARS in West, Central and eastern Africa was an important tool for this work. Within the network, in-depth investigations were undertaken at many sites covering a range of trypanotolerant and trypanosusceptible livestock breeds under different levels of tsetse/trypanosomiasis risk and management. ILRAD scientists recognized the trypanotolerant attributes of certain breeds of *B. taurus* (humpless cattle), specifically the N'Dama. Despite evidence from the ATLN that N'Dama could be productive under trypanosome challenge without treatment, there remained reluctance among farmers in East Africa to adopt the N'Dama because of its small size and low milk yield. This helped to draw attention to the trypanotolerance promise (based on early field results) of a particular Zebu cattle breed, the Orma Boran of East Africa. Farmer interviews at the time already suggested that introducing tolerance into larger breeds of cattle, including improved exotic (European) breeds, would be acceptable, and this held promise as a way to use trypanotolerance traits (see Chapters 2 and Chapter 3, this volume).

In a search of genetic markers for trypanotolerance, two polymorphic systems of bovine lymphocyte antigens were studied in 1988 by ILRAD in collaboration with ILCA. These systems were the MHC and a more limited polymorphic system of common leucocyte antigens, detected in cattle only. The first objective of the study was to survey the MHC and common leucocyte antigen phenotypes of populations of N'Dama cattle in Zaire and The Gambia and to compare these phenotypes with corresponding profiles of trypanosensitive Boran cattle in Kenya. The second objective was to look for associations between these MHC and common leucocyte antigen phenotypes, trypanotolerance and the productivity of N'Dama cattle. Significant correlations were found between the two classes of lymphocyte markers and the degree of resistance shown by trypanotolerant cattle exposed to trypanosomiasis by natural challenge. These results, which suggested the existence of genetically selectable markers for the trypanotolerant trait, were investigated further using larger numbers as well as family groups of cattle. The results indicated a central role for immunity in the manifestation of the trypanotolerant trait.

From 1987, N'Dama heifers produced at ILRAD from frozen N'Dama embryos brought in 1983 from The Gambia were regularly induced to superovulate using Folltropin, a follicle-stimulating hormone (Jordt and Lorenzini, 1990). By implanting the best of the N'Dama embryos in Boran foster mothers, ILRAD produced 24 N'Dama calves, which were used in studies of trypanotolerance and bovine genetics.

In the 1990s, ILRAD scientists undertook research to identify molecular mechanisms or markers for defining trypanotolerant cattle types – polymorphisms that differentiate breeds such as the N'Dama and Baoulé (both *B. taurus*)

from non-trypanotolerant African Zebu types. This work, among other things, examined variation in products of the MHC loci, biochemical variants of a variety of gene products, and both mitochondrial and nuclear DNA polymorphisms. Following an idea inspired by Morris Soller, of the Hebrew University of Jerusalem, to use molecular tools to map traits in cattle, ILRAD created a resource F_2 population segregating for trypanotolerance even before the technology was available for actual exploitation of such a resource population.

Among the early results were identification of informative polymorphisms, especially in the MHC, in the products of a small number of selected non-MHC loci, in nuclear satellite DNA and in a Y-chromosome sequence. This level of molecular and genetic characterization (Teale, 1993) provided what at the time was considered good differentiation of the major subspecies of cattle, providing a major transition from neutral to functional markers. The two marker types had previously been considered totally separate – 'fingerprinting' versus gene variants. It was anticipated that advances in molecular and computational technologies in the coming years would enable the examination and definition of genetic diversity beyond the subspecies level.

Informed by results of this early work, ILRAD and its collaborators (and other research groups that then entered this research area) focused on genome mapping to identify loci associated with QTLs, such as Taylor *et al.* (1998), who produced a genetic map of bovine chromosome 1, spanning more than 160 cM, with five laboratories contributing 31,962 informative meioses from 70 loci; Hanotte *et al.* (2003), who undertook F_2 mapping work, and Noyes *et al.* (2011), who identified candidate genes in pathways responding to *T. congolense* infection through genetic analysis and expression analysis of trypanosusceptible Kenyan Boran and trypanotolerant N'Dama cattle. Results of the F_2 mapping strongly supported a multi-locus model for the inheritance of trypanotolerance (Hanotte *et al.*, 2003). Trypanotolerance QTLs were found on 18 chromosomes, with an allele for resistance present at nine N'Dama QTLs and five Boran QTLs (Hanotte *et al.*, 2003). Multiple QTLs on several chromosomes were found to contribute to the three major tolerance indicators: anaemia, body weight and parasitaemia. Overall, the proportion of the phenotypic variance of the trypanotolerance traits explained by these QTLs remains relatively low. Moreover, the estimated effects of QTLs that are detected in experiments of only moderate power tended to be overestimated. This suggested the presence of other QTLs affecting trypanotolerance that are segregating in the N'Dama, as well as other QTLs with effects too small to be detected. To determine whether these QTLs could be used in marker-assisted selection, relevant genes or markers tightly linked to these would need to be resolved. Thus, as was the case with endoparasite resistance in sheep (see 'Genetics of resistance to gastrointestinal parasites'), traits that distinguish N'Dama and Boran cattle trypanotolerance proved to be regulated by multiple, unlinked genes (Box 1.2).

In parallel, the use of mouse models inspired by Alan Teale and the advanced intercross work led by ILRI collaborator Ariel Darvasi (Hebrew University of Jerusalem) led to the mouse F_2 (Kemp *et al.*, 1997) and F_6 (Iraqi *et al.*, 2000) fine mapping of trypanosomiasis resistance loci in murine. ILRI researchers identified here three areas of the genome that contributed to the control of resistance to trypanosomiasis, a result that represented the first mapping of QTLs controlling resistance to a haemoparasitic disease of major economic importance (see Chapter 2, this volume). More recently, demonstration of trypanosomiasis resistance in transgenic mice laid a strong foundation for subsequent research on ILRI's 'Mzima cow' project and related goat and chicken transgenics and biodiversity work. It awakened the possibility of using existing immunity to engineer new therapies and transgenic livestock (Willyard, 2011) and inspired the concept of transgenic livestock in which the ILRI cattle/mouse genome mapping group linked up with human trypanosomiasis resistance research.

All of the above results, over time, generated various levels of scientific impacts by enabling the evaluation of performance under challenge rather than reliance on indicator traits, an approach with potential to improve efficiency in genetic modification with selection *in situ*. Indeed, one of the original polymorphisms in N'Dama cattle is currently being selected for at the ILRI research station at Kapiti, Kenya.

Box 1.2. Mapping trypanotolerant QTLs in African cattle.

To identify QTLs controlling resistance to trypanosomiasis in cattle, ILRI made an experimental cross between trypanotolerant African N'Dama (*B. taurus*) and trypanosusceptible improved Kenya Boran (Zebu) cattle (Hanotte *et al.*, 2003). Sixteen phenotypic traits were defined describing anaemia, body weight and parasitaemia. In total, 177 F_2 animals and their parents and grandparents were genotyped at 477 molecular marker loci covering all 29 cattle autosomes. Total genome coverage was 82%. Putative QTLs were mapped to 18 autosomes at a genome-wide false discovery rate of less than 0.20. The results were consistent with a single QTL on 17 chromosomes and two QTLs on BTA16 (*Bos taurus* chromosome 16). Individual QTL effects ranged from approximately 6% to 20% of the phenotypic variance of the trait. Excluding chromosomes with ambiguous or non-trypanotolerance effects, the allele for resistance to trypanosomiasis originated from the N'Dama parent at nine QTLs and from the Kenya Boran at five QTLs, and at four QTLs there was evidence of an overdominant mode of inheritance. These results suggested that selection for trypanotolerance within an F_2 cross between N'Dama and Boran cattle could produce a synthetic breed with higher trypanotolerance levels than the parental breeds.

Noyes *et al.* (2011) provided both the method and the pathway from QTL analysis to SNPs by combining analytics pipelines. Researchers analysed the transcriptomes of trypanotolerant N'Dama and susceptible Boran cattle after infection with *T. congolense*, followed by sequencing expressed sequenced tag libraries from these two breeds to identify polymorphisms that might underlie previously identified QTLs, and assessed QTL regions and candidate loci for evidence of selective sweeps. They identified a previously undescribed polymorphism in trypanotolerance QTLs that affected gene function *in vitro* and candidate genes by their expression profile and the pathways in which they participate (Box 1.3).

Box 1.3. Candidate genes involved in the response to *T. congolense* infection.

Scientists used three strategies to obtain short lists of candidate genes within QTLs that were previously shown to regulate the response to infection (Hanotte *et al.*, 2003). They analysed the transcriptomes of trypanotolerant N'Dama and susceptible Boran cattle after infection with *T. congolense*; they sequenced expressed sequenced tagged libraries from these two breeds to identify polymorphisms that might underlie previously identified QTLs and assessed QTL regions and candidate loci for evidence of selective sweeps (Noyes *et al.*, 2011). The scan of the expressed sequence tags identified a previously undescribed polymorphism in the *ARHGAP15* gene in the BTA2 trypanotolerance QTL. The polymorphism affects gene function *in vitro* and could contribute to observed differences in expression of the mitogen-activated protein kinases (MAPK) pathway *in vivo*. The expression data showed that Toll-like receptor (TLR) and MAPK pathways responded to infection and the former contained TLR adaptor molecule 1 (TICAM1) located within a QTL on BTA7. Genetic analyses showed that selective sweeps had occurred at the *TICAM1* and *ARHGAP15* loci in African taurine cattle, making them strong candidates for the genes underlying the QTL. Candidate QTL genes were identified in other QTLs by their expression profile and the pathways in which they participate.

Genetics of resistance to gastrointestinal parasites

Helminthiasis is of considerable significance in a wide range of agroclimatic zones in Africa and Asia, as well as in other developing regions of the world. This disease constitutes one of the world's most important constraints to small-ruminant production (ILCA, 1991; Over *et al.*, 1992). The widespread occurrence of infection of grazing animals with internal parasites, the associated loss of production, the costs of anthelmintics and the death of infected animals are some of the major concerns that drew ILRI's attention in the early 1990s. In addition, there were (and still are) environmental concerns influencing anthelmintic usage, including consumer demand for animal products and pastures free of chemical residues. The high cost of anthelmintics, their uncertain availability, the increasing frequency of development of drug resistance and the limited scope in many communal pastoral

systems for controlled grazing (Mwamachi *et al.*, 1995; Waller, 1997) further limit options for controlling this disease. In the 1990s, it was considered unlikely that new broad-spectrum anthelmintics and vaccines would be available and accessible to smallholders. Utilization of host genetic variation for resistance was considered a more viable and sustainable approach to the control of internal parasites.

ILRI conducted in-depth reviews (Baker *et al.*, 1992, 1994a,b; Baker, 1998) to develop strategies for this work. The best documented examples of sheep breeds showing resistance to endoparasites in Africa were the Red Maasai sheep of East Africa and the Djallonké sheep of West Africa (Preston and Allonby, 1978, 1979; Baker *et al.*, 2003, 1994b; Baker, 1995). Informed by this review, ILRI initiated an ambitious research programme on the characterization of African small ruminants for genetic resistance to endoparasites. Evidence of genetic variation in sheep and goats for resistance to, or tolerance of, gastrointestinal nematodes had first been documented 40–50 years earlier and comprehensively reviewed by Gray (1991) and Gray and Woolaston (1991). Although the reviews provided evidence for a genetic basis of resistance to endoparasites, both between and within breeds of certain sheep and goat populations, almost all published reports available at the time suffered from inappropriate experimental design, particularly in terms of small sample sizes (numbers of animals of each breed sampled) and lack of information on how the animals had been sampled. The evidence for genetic variations in resistance to endoparasites within breeds was, at this point, more convincing, with heritabilities averaging about 0.35.

With the objective of investigating and characterizing genetic resistance to endoparasites in indigenous African sheep and goat breeds, the programme (ILCA, 1991) studied Dorper and Red Maasai sheep and Galla and Small East African goats in coastal Kenya; and Menz and Horro sheep breeds in the highlands of Ethiopia. It was envisaged that a second phase of the programme would investigate – by examining groups of animals that were most resistant and most susceptible – the immunological and genetic mechanisms controlling resistance to endoparasites. This work was expected to lead to identification of immunological or genetic markers of resistance. By 1992, the initial studies in coastal Kenya that were started before the launch of the major continent-wide programme (Reynolds *et al.*, 1992) were already showing clear signs that the local Red Maasai sheep were more resistant to endoparasites than the introduced Dorper sheep breed.

Building on the Red Maasai and Dorper herds already established at the Diani Estate of Baobab Farm, located some 20 km south of Mombasa, ILRI scientists established several genetic groups to facilitate the planned experiments. In addition to pure lines of the two breeds, a double backcross population of Red Maasai and Dorper sheep was also created (with the ultimate goal of identifying QTLs controlling resistance to gastrointestinal nematode parasites, mainly *Haemonchus contortus*). Under the same programme, a goat flock was also established and used for a study from 1994 to 1996 to compare the resistance to naturally acquired infections of gastrointestinal nematodes (predominantly *H. contortus*) of the Galla and Small East African goats in the subhumid coastal region of Kenya.

Three possible approaches for breeding for resistance are: (i) breeding for resistance (reduced parasite numbers, as determined by faecal worm egg count); (ii) breeding for resilience (ability to produce under parasite challenge, as measured by packed cell volume); and (iii) breeding for the number of treatments required during parasite infection (Woolaston and Baker, 1996). The two traits used by the ILRI team in all the studies were faecal worm egg count and packed cell volume.

Resistance to gastrointestinal nematodes in Red Maasai sheep

Red Maasai sheep and three-quarter Red Maasai lambs were consistently more resistant (lower faecal egg count) and more resilient (higher packed cell volume) than the Dorper and three-quarter Dorper sheep. The difference between the backcrosses for both faecal egg count and packed cell volume was about half of the difference between the purebred Red Maasai and Dorper lambs, indicating additive gene action. Moreover, even in artificial challenge experiments where there were no significant genotype differences in faecal egg counts, the Red Maasai and the three-quarter Red Maasai lambs had

significantly fewer worms than the Dorper and three-quarter Dorper animals.

An experiment was conducted in two environments – coastal subhumid and semi-arid – to examine genotype–environment (G×E) interactions for both productivity and resistance to gastrointestinal nematodes (Baker *et al.*, 2004). Here, too, the Red Maasai were consistently more resistant and more resilient in both environments than the Dorper sheep, but there were significant G×E interactions for ewe reproductive performance, ewe and lamb mortality rates, and live weights. Overall, taking together live weights, reproductive performance and mortality, the Red Maasai breed was considerably more efficient than the Dorper sheep in the subhumid environment, while in the semi-arid environment, there was a negligible breed difference in productive efficiency.

In a simulation study examining opportunities for using the Red Maasai breed resource for cross-breeding versus pure breeding, König *et al.* (2017) concluded that cross-breeding with Dorper sheep was not recommended for harsh environmental conditions due to the large breed differences expected in such an environment, while the breed could be improved through within-breed selection (e.g. applying a nucleus breeding scheme),

Taken together, studies done on the Red Maasai by the ILRI team and partners have unequivocally demonstrated, on the basis of indicators that collectively provide a reasonably reliable picture of resistance – faecal egg count and packed cell volume – that the Red Maasai perform significantly better than Dorper sheep under gastrointestinal nematode challenge. Moreover, the associated lowered mortality rates in the breed lead to much faster flock growth and productivity. Heritability estimates for packed cell volume and faecal egg count (Baker *et al.*, 2003) point to the use of different traits for selection: within the Red Maasai breed, the focus should be on resilience (i.e. selection for high packed cell volume), while for the Dorper selection, it should be feasible for both improved resistance (low faecal egg count) and resilience (high packed cell volume).

Menz versus Horro sheep of Ethiopia

Inspired by the Red Maasai results in Kenya, similar studies were initiated in Ethiopia, where Menz and Horro sheep were compared on-station in a highlands environment (Rege *et al.*, 1996; Haile *et al.*, 2002; Rege *et al.*, 2002). The predominant gastrointestinal parasites at this location are *Longistrongylus* and *Trichostrongylus* spp. There was no difference in resistance to parasites between the Menz and Horro breeds as reflected by faecal egg counts. While packed cell volume is a useful indicator of resistance when *H. contortus* is the predominant gastrointestinal parasite, this was not the case in this highland site in Ethiopia. Thus, although the Menz lambs had a significantly higher packed cell volume than Horro lambs, this could not be related to their resistance to endoparasites and was instead attributed to an adaptation of this breed to higher altitude (their original habitat). The Menz lambs had significantly lower mortality than Horro lambs both pre- and post-weaning, which was also considered a reflection of their better adaptation to the high-altitude environment.

Small East African versus Galla goats

Results of experiments examining gastrointestinal nematode resistance in goats (Baker *et al.*, 1998a,b, 2001) showed that the Small East African kids were more resistant to gastrointestinal nematode parasites than Galla kids, with the former having significantly lower faecal egg counts in the post-weaning period (8–14-month-old kids) and lower mortality from birth to 14 months of age. However, there was no significant breed effect on packed cell volume, but Galla kids were significantly heavier at all measurement times between birth and 14 months. However, heritability estimates were generally low at 0.18±0.08 (mean±se) for packed cell volume and 0.13±0.07 for faecal egg counts.

ILRI studies inspire and provide benchmarks for national experiments

The sheep breeds used in the various ILRI studies have subsequently been widely used in other studies, and interpretations of results suggest that these early studies by ILRI served as benchmarks or references for similar research in Africa. For example, using Dorper sheep in their experiments, Matika *et al.* (2003) found Sabi sheep of Zimbabwe to be more resistant than the Dorper – the proportion of Dorper ewes needing

treatment with antihelmintics was significantly higher than that of Sabi ewes at all sampling dates, and this effect was particularly marked at 1 and 2 months post-lambing. Getachew *et al.* (2015) compared the Menz sheep breed with the Washera breed in the highlands of Ethiopia and found that Menz sheep were better able to maintain live weight during the parasite challenge, while Eguale *et al.* (2009) compared the Arsi sheep breed with both Menz and Horro on resistance to liver fluke infection and concluded that the Horro breed was more resistant than Menz and Arsi in that environment. Like the Red Maasai in eastern Africa, the Djallonké stands out in various studies in West Africa as the breed with the most compelling evidence of parasite resistance (e.g. Traoré *et al.*, 2012; Soudré *et al.*, 2018).

Following publication of the early ILRI results on goats, the West African Dwarf goat drew attention; studies demonstrated that, like its sheep counterpart the Djallonké, it was a promising candidate breed for genetic resistance to gastrointestinal nematodes (e.g. Chiejina *et al.*, 2010; Behnke *et al.*, 2011).

Link between resistance and productivity

In addition to evidence for between-breed differences in resistance to endoparasites, these studies also provided the first hard evidence of genetic variation within breeds of sheep and goats in Africa, i.e. significant heritability estimates strongly pointing to opportunities for within-breed improvement of this trait through selection. Specifically, the results confirmed that Red Maasai sheep and Small East African goats are more resistant to gastrointestinal nematode parasites (predominantly *H. contortus*) than Dorper sheep and Galla goats, respectively. The resistant Red Maasai sheep and Small East African goats were also two to three times more productive than the susceptible Dorper sheep and Galla goats in the subhumid coastal Kenya environment.

With the formation of ILRI in 1995, some new research initiatives were undertaken in South-east Asia, including work led by a small ILRI team based in the Philippines and involving ten countries. The objectives of the Australian Centre for International Agricultural Research (ACIAR)-supported project were: (i) to assess anthelmintic resistance in gastrointestinal nematode parasites (worms) of sheep and goats and to investigate methods of blocking their spread; (ii) to assess genetic variation in resistance to worms in indigenous and imported breeds of sheep and goats; and (iii) to disseminate information about control of worms in sheep and goats in the tropics. Interventions investigated included the strategic use of anthelmintics, the usefulness of ethnoveterinary therapies, biological control, improved nutrition, grazing management and housing, and utilizing local indigenous breeds with at least some resistance to worms. The results of this research are summarized in Sani *et al.* (2004). This work established that importation of purebred Merinos was not a good idea because of their susceptibility to worms, but that imported St Croix sheep showed resistance and adaptability to tropical conditions. In goats, the native goats in the Philippines and imported Boer goats were somewhat more resistant than imported Anglo-Nubian and Saanen goats. A key achievement of this work was the design and testing of integrated worm control programmes in a number of different countries and management systems in South-east Asia.

QTLs for resistance to endoparasites in small ruminants

The existence of within-breed variation strongly suggested that selection for nematode resistance in sheep (and goats) in breeding schemes would help to reduce the direct and indirect costs of parasitism to production. However, this is not widely practised because of the difficulty of measuring parasite resistance or correlated indirect selection criteria. It was considered, therefore, that identifying genes or linked markers with a significant association with the variance of indicator traits of internal nematode resistance in sheep would facilitate the inclusion of nematode resistance in breeding operations. New technologies were already becoming available that could be applied for breeding purposes if the genes or QTLs involved in parasite resistance or markers that are closely linked to these genes could be identified.

The hunt for QTLs (Silva *et al.*, 2011; Marshall *et al.*, 2013; Benavides *et al.*, 2015) did not point to a definitive region as an obvious candidate for selection. Several genomic regions featured in the search for markers for nematode resistance in sheep, and genomic regions that

have been identified as being significantly associated with indicator traits for nematode resistance vary widely among studies. This could be due to differences in experimental protocols and materials (studies differed in the sheep breeds and nematode species, the indicator traits for internal nematode resistance, and the challenge regimes), differences in the analytical approaches, population stratification, complexity of the physiological processes of nematode resistance or a combination of factors. Sayers and Sweeney (2005) reported similar results for the MHC genes, interferon-γ gene, IgE gene and microsatellites on chromosomes 1, 5 and 6. Crawford *et al.* (2006) reported a large number of suggestive QTLs (more than one per family per trait than would be expected by chance) and concluded that most of the genes controlling this trait are of relatively small effect. Marshall *et al.* (2009) suggested that where traits are controlled by multiple QTLs (such as age and/or immune status specificity in Merino sheep), a panel of QTLs is required to achieve significant genetic gains through marker-assisted selection.

Alba-Hurtado and Muñoz-Guzmán (2013) noted that genetically resistant sheep have non-specific mechanisms that block the initial colonization by *H. contortus* larvae, and that they also have an efficacious response of T-helper type 2 cells (e.g. increases in blood and tissue eosinophils, specific IgE class antibodies, mast cells, interleukin-5, interleukin-13 and tumour necrosis factor) that protect them against the infection. The use of a mouse model to help the genome-wide search for QTLs influencing immunological responses to infection with the gastrointestinal nematode (in this case the parasite *Heligmosomoides polygyrus*) did not help either (Iraqi *et al.*, 2003; Menge *et al.*, 2003; Behnke *et al.*, 2006). Here, too, many genomic regions with small effects were implicated.

Thus, although there are some genomic regions that have featured in multiple studies across breeds (e.g. the interferon-γ region on chromosome 3 has come up as influencing a significant proportion of the variance for nematode resistance traits by multiple authors; e.g. Coltman *et al.*, 2001; Paterson *et al.*, 2001; Beh *et al.*, 2002), there really is no compelling convergence on one or a few regions that explain the large variation in resistance. Currently, there is no evidence pointing to the possibility of establishing a breeding programme focusing on one or two genomic regions. Having realized that there was no major gene (or small number of genomic regions with large effects) involved in conferring resistance to gastrointestinal nematodes, and that there were instead many genes/genomic regions, each with small effects, a multi-trait selection programme was initiated at ILRI's Kapiti Ranch for both Red Maasai and the Dorper × Red Maasai crosses, under natural and continuous challenge (see section on 'Genetic improvement of livestock').

DAGRIS

Information on the extent of diversity, characteristics and use of indigenous farm AnGR in developing countries is the basis for their present as well as future sustainable utilization. Published data on this diversity were disparate, uncoordinated and largely inaccessible. In view of the lack of a systematic database on this information, ILCA initiated development of the DAGRIS in 1993 as a web-based electronic source of information on selected indigenous farm AnGR (Rege *et al.*, 2007). This was an important product of genetic characterization work over the years and into the future. The working objectives of DAGRIS were to: (i) compile and organize information on farm AnGR from all available sources; (ii) maintain the integrity and validity of the information; and (iii) disseminate the information in a readily accessible way to key stakeholders. Today, DAGRIS has information on breeds/strains of eight species, namely, buffalo (139 breeds/strains), cattle (189), chickens (126), dromedary camels (10), goats (83), pigs (166), sheep (179) and yak (30), with options to extend it further to cover geese, turkey and ducks. Its current geographical scope is Africa and selected Asian countries, with an envisaged future coverage of developing countries in Asia and Latin America and the Caribbean.

The database contains information on the origins, distribution, diversity, present use and status of indigenous farm AnGR from past and present research results, information that can be used to form the basis for designing breed improvement as well as conservation programmes. DAGRIS is available online (http://dagris.ilri.cgiar.org; accessed 28 January 2020) as well as

on CD-ROM, making it accessible even to those without internet connectivity. The utility of this resource is demonstrated by increasing trends in website visits and citation indices.

Biorepositories/biobank facilities

The Azizi Biorepository is the long-term storage system and associated informatics tools that comprise the biorepository at ILRI. The system supports and has supported a number of activities and projects, including 'Infectious Diseases of East African Livestock', 'Arbovirus Incidence and Diversity', 'People, Animals and their Zoonoses', 'Dynamic Drivers of Disease in Africa Consortium', 'African Bovine Trypanosomiasis', the ILRI livestock diversity collection and ILRI's unique collection of pathogen isolates. The core collection is approximately 450,000 samples in vapour-phase liquid nitrogen with uniquely robust, secure and well-monitored ultra-cold conditions for long-term storage. Samples and associated data collection are based on strict protocols and procedures to ensure that they meet the required and acceptable minimum standards. The repository provides a platform for researchers to mine samples and data that can be used in their research. This in turn means that expensively obtained samples can be used and re-used for additional purposes and that the metadata associated with each sample is continually enriched, thus enhancing efficiency. The repository approach also maximizes biological understanding as it facilitates different pieces of information about identical samples. In addition, samples and data in the repository are managed to ensure that they meet CGIAR requirements of open access. ILRI's Azizi Biorepository is the only one of its kind in sub-Saharan Africa for the products of long-term characterization work. It currently contains samples of a wide range of livestock species and breeds, wildlife, insects and disease-causing organisms. Samples are in various forms including blood, serum, milk, faecal material, DNA and RNA.

Economic valuation

In 1999, FAO and ILRI convened a workshop on 'Economic Valuation of Animal Genetic Resources' to provide expert guidance on valuing AnGR. In the face of strengthening laws for intellectual property protection of germplasm under the Convention on Biological Diversity, it was also becoming apparent that the past collegial system of free exchange of germplasm among researchers was going to break down fast, requiring that some mechanism (e.g. through mutually agreed terms) for genetic resources movement across borders would be needed, both for research and for commercial purposes. It was recognized that, because markets exist only for finished or nearly finished commercial genetic resources, the value of unimproved materials and the value added that were not 'valued by commercial interest' in the long process of breeding (including through efforts of indigenous communities) could not be measured directly. Yet this was going to be critical under the Convention on Biological Diversity regime, i.e. it was important that 'parties' (e.g. communities and countries) had a way of determining the values of the AnGR involved in an 'exchange', whether within countries or across borders. During the ILRI convening, Mendelsohn (1999) made at least three arguments for economic valuation of AnGR: (i) to inform breeding programmes; (ii) to guide choice of breeds in conservation programmes and (iii) to facilitate benefit sharing (in the context of the Convention on Biological Diversity). It was also considered that economic valuation would be instrumental in guiding resource allocation between biodiversity conservation and other socially valuable endeavours. Likewise, the results of valuation would be used in various types of genetic resource conservation, research and development, including in the design of economic incentives and institutional arrangements for farmers/genetic resource managers and breeders. For example, AnGR erosion could be understood in terms of the replacement of breeds and strains, not only by substitution but also through cross-breeding and the extinction of livestock populations.

Following the 1999 ILRI/FAO joint 'Economic Valuation of Animal Genetic Resources' workshop, ILRI initiated a programme on 'Economics of AnGR Conservation and Sustainable Use', focusing on valuation methodologies. The valuation dimensions covered included: risk of extinction as an important consideration for

allocating conservation resources (Reist-Marti *et al.*, 2003; Simianer *et al.*, 2003); farmer preferences (Jabbar and Diedhiou, 2003; Duguma *et al.*, 2011); trader preferences (Scarpa *et al.*, 2003a); effects of subsidies of local and imported germplasm (Drucker *et al.*, 2006); value and impact of cross-breeding (Karugia *et al.*, 2001; Ayalew *et al.*, 2003); valuation in the context of community-based management of AnGR (Drucker, 2003); specific genetic resources for specific environments (Scarpa *et al.*, 2003b; Omondi *et al.*, 2008); and influence on policy (Drucker, 2010). An important goal of the economic valuation of AnGR is the development of policies and strategies for conservation and sustainable utilization of these resources. Economic valuation tools were also seen as contributing to the development of policies and strategies for conservation and use by providing critical information for decision making in this domain. Of particular interest was the situation in developing countries, where, on the one hand, livestock make important contributions to human livelihoods and food security, while on the other, genetic erosion was placing at risk many breeds adapted to the low-input agriculture and extreme environments typical of these countries. For example, although their productivity in absolute terms is lower than commercial breeds under intensive production systems, indigenous AnGR are often the only option available for millions of farmers in the African agropastoral systems, where exotic improved breeds underperform (if they survive) in traditional management systems.

Tools for conservation decisions

Valuation studies undertaken by ILRI and partners have provided tools and methods for valuation that can be broadly applied. Choice experiments were found to be a promising tool for valuing phenotypic traits expressed by indigenous AnGR (Scarpa *et al.*, 2003a), while the Weitzman approach was found to be a potentially effective methodology for determining conservation strategies under highly varying circumstances and for many species (Reist-Marti *et al.*, 2003). Simianer *et al.* (2003) proposed a functional relationship between conservation funds spent in one population and the conservation effect in terms of reduced extinction probability. The results indicated that, in some cases, highest priority could be given to breeds for which the 'conservation potential' (i.e. the product of extinction probability and marginal diversity) is maximum, and that these are not necessarily the most endangered breeds.

Some of the results of this work have pointed to the fact that conservation goals can be generally modest (FAO, 2013), and in view of some of these findings, it has been estimated that the 'not at risk' status category (as applied in the FAO recommended framework) requires 2000 breeding females in species with high reproductive capacity and 6000 in species with low reproductive capacity. This suggests that the costs of conserving a priority portfolio of at-risk breeds may also be quite modest (Drucker, 2010). An assessment of public willingness to pay for conservation by Zander *et al.* (2013) and estimates of the support payments that would be required to achieve the stated conservation goals suggest that such conservation costs may well be both economically justifiable (benefits outweighing costs) and relatively low cost. Thus, conservation costs may be overestimated if based only on conventional economic opportunity cost estimates, especially considering findings by Krishna *et al.* (2013), which suggested that farmer willingness to participate in genetic resources conservation activities for the public good may be more closely related to the consumption values of the genetic resources in question than to their production opportunity costs (which generally do not take into account the existence of farmers' many non-market preferences and values).

ILRI's work in this area has received recognition. The first report on 'The State of the World's Animal Genetic Resources for Food and Agriculture' (first SoW-AnGR; FAO, 2007) included a section on methods for economic valuation with an overview of the various types of value (direct and indirect use values, option values, bequest values and existence values) and described potential methods and tools for assessing them, with explicit reference to work done by ILRI and examples of the use of these methods and tools and the findings obtained on the methods. The second SoW-AnGR (in 2015) focused on economics of use and conservation, reflecting and explicitly recognizing advances that

had been made on valuation methodologies during this period. It has been recognized, for example, that accounting for total economic value can determine, among other things, whether the benefits of intervention outweigh the costs, as well as appropriate intervention strategies, including for situations in which specific AnGR have little or no current market-development potential. Where conservation funds are limited, understanding the 'true' (i.e. total) economic value of different breeds and their contribution to the public good can be an important tool in priority setting and allocation of funds (Fadlaoui *et al.*, 2006). An understanding of the relative values of the different components of total economic value can also be used to provide insight into the viability of different use and conservation strategies, such as identification of the relevance of different types of economic value and associated ecosystems services to different stakeholder categories and their willingness to pay for the services provided by the maintenance of breeds (Zander *et al.*, 2013). Indirect use values, such as cultural and landscape maintenance values, are likely to be of more relevance to local communities, while option values are likely to be of relevance to a much broader range of stakeholders. To maximize societal welfare, strategies for conservation through active use need to be designed with a view to maintaining the ongoing provision of the public-good breed-related functions that people value most (Martin-Collado *et al.*, 2014).

Genetic Improvement of Livestock

Cross-breeding of indigenous livestock with exotic breeds has for a long time been considered a faster way of making genetic improvements and one that is simple because it does not require the same level of performance and pedigree recording as selection. However, inadequate nutrition and the presence of significant biotic and abiotic stresses, including poor management, have continued to limit the use of high-input exotic breeds of livestock and their crosses, and is largely why many farmers in Africa still keep the more resilient indigenous livestock breeds. There have been only a few success stories of within-breed improvements of indigenous breeds.

The productivity potential of native livestock breeds under various systems remains largely unexploited. This, plus the fact that cross-breeding is considered to produce faster results, has informed the widespread practice of upgrading indigenous breeds through cross-breeding using imported breeds, particularly for milk and meat production. East Africa (especially Kenya but also Ethiopia, Rwanda, Tanzania and Uganda to smaller extents) leads other sub-Saharan African regions such as West Africa in the use of cross-breeding, especially for generating 'grade' cows used in smallholder dairy systems. However, cross-breeding is also widely applied in beef systems in southern Africa and in sheep and goats as well as in chickens across the African continent. In addition to upgrading, systematic programmes aimed at creating new synthetic or composite breeds apply a combination of planned cross-breeding and selection. Kenya, like South Africa, has had programmes aimed at developing dairy goats – the Kenya dual-purpose goat and the Meru goat (Ojango *et al.*, 2010) – through systematic cross-breeding.

Other than its work on genetics of tolerance to trypanosomiasis, ILRAD's mandate did not include genetic improvement of livestock. For its part, despite a broader mandate on livestock production, ILCA's first-generation programmes in the 1970s and 1980s had a more diagnostic orientation – 'understanding African livestock systems'. However, aspects of breeding were introduced through work started by John Trail and colleagues on quantifying performance in smallholder and pastoral systems (e.g. Trail, 1981; Trail and Gregory, 1981, 1982; Trail *et al.*, 1982, 1984, 1985) and by NARS visiting scientists and collaborators (Kiwuwa *et al.*, 1983; Tawonezvi *et al.*, 1988a,b) recruited specifically for that purpose. The ILCA Strategy and Long-Term Plan from 1987 was more explicit in its attention to animal genetics and breeding. In this plan, the Cattle Milk and Meat Thrust included a sub-theme on 'evaluation of the genetic potential of cattle breeds and their crosses for milk and meat production', while that of Small Ruminant Meat and Milk included 'evaluation of small ruminant genetic resources to identify appropriate breeding strategies'. The Trypanotolerance Thrust committed to the collection and analysis of data on the productivity of trypanotolerant

breeds under various levels of trypanosomiasis risk, and definition of selection criteria for trypanotolerance (see Chapters 2 and 3, this volume), to devise optimum breeding programmes. Through these activities, mostly implemented in partnership with NARS, ILCA helped to analyse and publish data sets characterizing cattle and small-ruminant populations in Africa on the basis of performance traits, and ILRAD and ILCA led efforts in collaboration with NARS, ITC and CIRDES, among many partners, to document trypanotolerance traits in cattle and small ruminants. ILCA's breed comparisons were done principally by assisting NARS scientists to analyse on-farm and on-station data. In 1989 and 1990, ILCA recruited visiting scientists[1] and provided other support to sub-Saharan African countries in interpretation of breeding data (e.g. Mwenya, 1990).

Analysis of long-term breeding programmes

Much of this early work emphasized breed/genotype evaluations to provide information on how different indigenous African livestock breeds and their crosses performed under different management systems (e.g. Rege *et al.*, 1993a,b,c; Tawah *et al.*, 1993; Thorpe *et al.*, 1993; Moyo *et al.*, 1996; Kurtu *et al.*, 1999) or to assess the effectiveness of long-term national breeding programmes in terms of genetic progress made, for example, in cattle (e.g. Rege, 1991; Rege and Wakhungu, 1992; Tawah *et al.*, 1994) and sheep (Yapi *et al.*, 1994; Yapi-Gnaorè *et al.*, 1997a,b), the latter being through an Open Nucleus Breeding System (Box 1.4). ILRI also contributed to the evaluation of two composite breeds in Tanzania: the Mpwapwa cattle (Kasonta, 1992) and the blended goat (Das *et al.*, 1996).

Apart from informing breeding policies within sub-Saharan African countries, some of these studies also made methodological contributions as well as human capacity strengthening for the region. For example, the weight of calf weaned per 100 kg metabolic body weight of cow exposed to the bull was examined as a possible approach for adjusting for differences in maintenance requirements by different cow genotypes, thus providing a 'fair comparison' between small-bodied indigenous breeds and large-bodied exotic breeds and crosses (the belief that local breeds were small and not as good drove importations of exotic breeds); the effect of date of birth on growth performance in seasonally bred beef cows was examined as a means of determining the optimum breeding time in such systems (Rege and Moyo, 1993); and a method was proposed for estimating between-breed differences in cross-breeding parameters and their sampling variances in these systems (Rege *et al.*, 1993a). Recommendations based on in-depth analyses of the Sahiwal Stud of Kenya (Rege and Wakhungu, 1992) and the Kenya Dairy Cattle Improvement Program using long-term data provided evidence that informed changes in these breeding programmes, such as a decision to open the Sahiwal Stud herd (which until then had been a closed herd) to bring in new breeding stock to reduce inbreeding levels and to broaden

Box 1. 4. Open Nucleus Breeding System for sheep improvement in West Africa.

A selection programme was set up in 1983 in Côte d'Ivoire to improve the growth and live weight of the indigenous Djallonké sheep using an Open Nucleus Breeding System (Yapi *et al.*, 1997a,b). Selection was based on male individual weights at 80, 180 and 365 days of age. Multiple sires were used in farmers' flocks. ILCA helped to analyse this programme in 1995/6. Individual animal models using an average numerator relationship was used to estimate breeding values from which genetic trends were derived. A total of 10,417 records of 80-day weights (WT80) of lambs born between 1984 and 1992 from 29 participating farmers, and 1978 and 849 records on 180-day weights (WT180) and 365-day weights (WT365), respectively, of lambs from the nucleus were analysed. Breeding values – as a measure of genetic trends – increased by 28, 11 and 14 g/year for WT80, WT180 and WT365, respectively. The results of the study indicated that genetic progress could be made in growth performance of indigenous sheep if reasonable levels of animal management as well as selection pressure are applied in the Open Nucleus Breeding System and suggested that community-based breeding schemes had potential for genetic improvement in small-ruminant populations in these systems.

the genetic base, and a reorganization of the Kenya National Dairy Breeding Plan and its management. In all cases, the collaboration with NARS scientists was in-built and used to provide training on aspects of design and analysis of livestock breeding programmes.

Towards the optimization of breeding programmes in Africa

ILCA scientists worked with NARS in the 1980s on breed comparison studies, which focused on cattle (both dairy and beef) and small ruminants. The finding by early researchers (e.g. Kiwuwa *et al.*, 1983) of similarity in performance of the 75% and 50% *B. taurus* crossed with African Zebu was among the first (based on a large data set covering 1968–1981) to signal that there was a 'limit to upgrading' and that this limit depended on the production system. Marshall *et al.* (2017) showed that exotic dairy cattle under good management do have higher milk yields than local × exotic crosses, but the additional cost of feed is such that local × exotic crosses are more profitable. A similar project implemented in West Africa – the Senegal Dairy Genetics project – resulted in strong recommendations on the best genotype in Senegal dairy systems, based on a trade-off perspective (Salmon *et al.*, 2018). These studies plus evidence from genetic diversity research have induced a gradual recognition that 'upgrading towards exotic genotypes' across all systems is a mistake and that indigenous genetics should play an important role in breeding programmes.

The challenge to genetic improvement, however, goes well beyond the choice of breeds. Institutional and organizational challenges are as binding as genotype in many African countries (Kosgey, 2004; Kosgey and Okeyo, 2007; Rege *et al.* 2011). Consequently, even cross-breeding practice, considered to be easier than within-breed selection, has generally not been well-planned in Africa and outcomes have been inconsistent. Many cross-bred populations, including the dairy herds in Kenya and other East African countries where cross-breeding for dairy production is considered a success, tend to be a mix of genotypes (Aliloo *et al.*, 2018; Mrode *et al.*, 2018). The so-called 'grade' or cross-bred animals in smallholder systems in Kenya, for example, are composed of a wide range of genotypes, and in the absence of pedigree records, genotypes of individual cross-bred animals are generally unknown.

These challenges have informed ILRI's recent work in 'genetic improvement'. One problem has been determination of optimum genotypes for specific production systems. Figure 1.2 illustrates levels of milk production by different

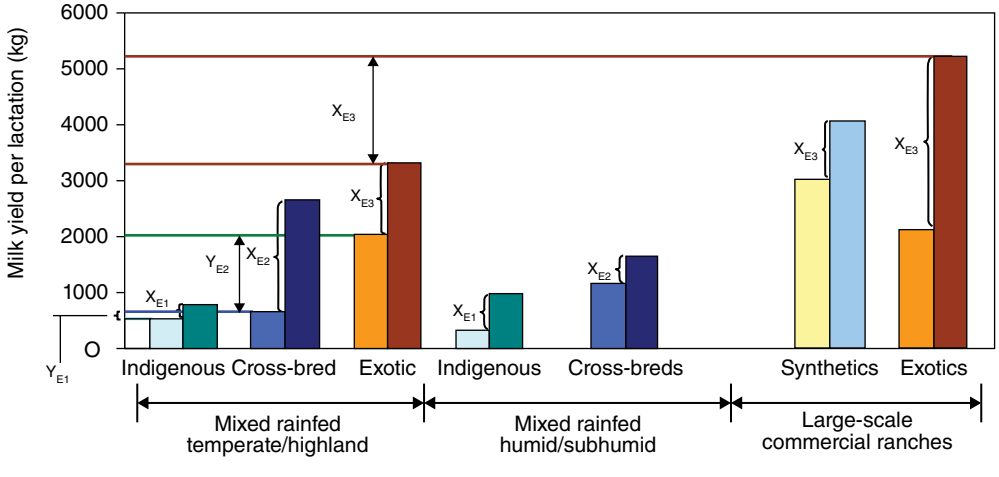

Fig. 1. 2. Milk production by genotype in dairy production systems of eastern Africa. Light-coloured bars, minimum production; dark-coloured bars, maximum production; x_i, differences in production due to 'animal husbandry practices'; y_i, differences in production due to 'genotype'. (From Mwacharo *et al.*, 2009.)

genotypes – indigenous, cross-breds, composite breeds and exotics – in dairy production systems in eastern Africa. The figure shows that cross-breeding certainly has a role to play and also illustrates the critical need for matching genotypes with production environments, especially considering that smallholder producers in these systems have little control over the many environmental and production factors/stresses that affect and constrain the productivity of their livestock. This was the compelling documentation of G×E presented in a way (yield gaps) that development partners can easily understand. Subsequent data from ILRI's own work (e.g. from the DGEA project) have not contradicted the general patterns in genotype comparisons but have shown diminishing returns to upgrading under smallholder systems (performance improvements beyond F_1 being rare in most situations).

Breeding programme design

There had been growing demand among NARS for ILRI engagement in: (i) non-ruminant livestock research, specifically chickens; and (ii) support for breeding programmes that went beyond analysis of existing information. In ILRI's long-term strategy to 2010 (ILRI, 2000), two decisions were made: (i) to expand the genetic characterization portfolio beyond cattle, sheep and goats to include, for the first time, an explicit commitment to 'contribute to the characterization of indigenous swine, poultry, camel, buffalo and yak populations in Africa and Asia'; and (ii) to engage more directly in 'developing breeding strategies to improve utilization of diversity of indigenous livestock to increase productivity in smallholder systems'. It is to be noted, however, that although there had not been a formal programme as such in this area up to this point, individual ILRI scientists were already contributing to breeding programme design, mostly through graduate student projects and fellowships (e.g. Kosgey, 2004; König *et al.*, 2017). Among the major activities initiated following the decision to engage in breeding programme design, four stand out: Two are in dairy – the DGEA and the African Dairy Genetic Gains (ADGG) projects – and two are in chickens – the Horro chicken improvement and the African Chicken Genetic Gains (ACGG) projects.

Appropriate germplasm for smallholder dairy farmers

The DGEA project was funded by the Bill & Melinda Gates Foundation. Determining the size of breed differences *in situ* (linking farmers' genotypes to productivity) was a core question of the DGEA project. The answer was expected to allow calculation of the net benefits of investment in germplasm delivery. Specifically, the DGEA project set out to answer two broad questions (Rege and Gibson, 2009): (i) what are the optimum breed combinations for smallholders in different production environments? and (ii) how can sustainable germplasm supply systems be developed?

Optimum breed combinations

High-density SNP technology was used to optimize choice among cross-bred dairy cattle in Kenya and Uganda, primarily for *in situ* assessment of the performance of existing genotypes (Ojango *et al.*, 2014). While SNP data accurately estimated breed composition, they only did so under very careful construction analyses and, as such, caution must be taken in applying their results in decision making.

Sustainable germplasm supply

The activities under sustainable germplasm supply involved the design, operation and support of an innovation platform, bringing together agents in the germplasm supply chain to smallholders. The innovation platform led to identification of business opportunities in dairy genotyping (specifically heifers and artificial insemination). Several local farmers and traders established businesses that identified sellers of heifers, found buyers, and built seller and buyer capacity in heifer management.

Supporting on-farm selective breeding by smallholders

The absence of breeding recording in developing countries has been a major limiting factor to systematic selective breeding in Africa (Kosgey and Okeyo, 2007; Zonabend *et al.*, 2013). Other limiting factors are poor breeding infrastructure and lack of good analytical tools (Gizaw *et al.*, 2014; Mrode *et al.*, 2018; FAO, 2016). It is now

well recognized that, unless recording is owned and run by industry (farmers themselves) with sufficient incentives to make them participate, it is unlikely that sustainable recording programmes can be achieved. This explains why the limited schemes remain restricted to the large commercial farming sector where owners recognize and are willing to pay for recording.

To address the recording challenge, ILRI, through the ADGG programme, in 2018/19 is supporting the establishment of farmer-driven ICT-based on-farm pedigree and performance recording in Ethiopia and Tanzania. The objectives of ADGG were to establish performance recording and sampling systems (FAO, 2016) to pilot farmer-feedback systems that help farmers improve their productivity, and to use the information and samples collected to develop systems for selecting cross-bred bulls and cows of superior genetic merit for artificial insemination and natural mating (König *et al.*, 2017). Informed by experiences of the DGEA project, the main thrust for this initiative is a digital platform for performance data capture/analytics that combines utilization of genomics to demonstrate and inform implementation of expanded genomic evaluation and better utilization of cross-bred cattle populations (see https://www.ilri.org/research/projects/african-dairy-genetic-gains). It is designed to collect and use on-farm performance information and basic genomic data to identify and provide superior cross-bred bulls for artificial insemination delivery and natural mating cows on smallholder farms. While at the time of writing the programme was still in the early stages, more than 82,000 smallholder herds and more than 190,000 animals were already being recorded on the platform in the two countries, with more than 5000 of these already genotyped and the results, together with the phenotypic records being used to generate genomic breeding value predictions (Brown *et al.*, 2016) in Tanzania and later in Ethiopia. Farmers on the platform received more than 6 million text messages in four languages to inform herd management decisions and benefitted from productivity gains.

Demonstrating potential for within-breed selection

In 2008, ILRI and Wageningen University started a pilot breeding project for Horro chickens in Ethiopia. What started as a 'proof of concept' has become a major success, the Horro chicken breed improvement programme in Ethiopia (Box 1.5), and has demonstrated that within-breed selection is possible in indigenous chickens. In November 2015, in recognition of these achievements, the prime minister of Ethiopia awarded the project the 6th National Science and Mathematics, Research and Innovation Award of Ethiopia.

The Horro chicken project, together with the community-based sheep and goat breeding program in Ethiopia (Box 1.6) and the Red Maasai and Dorper sheep breeding programme in Kenya (Box 1.7) are examples of success in establishing within-breed genetic improvement programmes. The improved Horro chicken was tested in the ACGG programme on-farm and on-station (Box 1.8). The aim was to compare the performance of this improved chicken in regions of Ethiopia with large differences in altitude, rainfall and temperature. The improved Horro chicken in the ACGG comparisons reached 714 g at about 16 weeks of age. Unimproved chickens could not reach the same live weight, even at 20 weeks of age and under improved management conditions. Moreover, the improved Horro chicken started egg laying at the age of 223 days compared with 256 days for unimproved indigenous chickens on-farm.

Towards adapted and productive chickens for African smallholders

Many past efforts to make smallholder chickens more productive in sub-Saharan Africa have not delivered optimal impact because they used high-producing commercial genotypes created for intensive temperate feeding systems. In collaboration with NARS in Ethiopia, Nigeria and Tanzania and involving several other partners, ILRI initiated a project (ACGG) in 2014 with the aim of identifying and delivering adapted chickens to support productivity growth and increased animal protein intake among rural people (Box 1.8). The key features of this project were: (i) a focus on delivery of farmer-preferred chicken genotypes; (ii) use of innovation platforms to identify chicken value chain challenges and to develop solutions in participatory processes involving key value chain actors;

Box 1.5. Horro chicken breed improvement programme in Ethiopia.

The Horro chicken breeding programme implemented by ILRI in collaboration with Wageningen University in Ethiopia started in 2008 as a PhD project of Nigussie Dana. The objective was to improve production of village chickens through participatory within-breed selection. The breeding objectives were identified using a participatory approach. The breeding programme aimed to develop a dual-purpose chicken through selective breeding. As a start, a survey was conducted to understand the production systems and the needs and constraints of smallholder chicken farmers in 225 households. The breeding goal traits identified were egg production (number), body weight, (decreased) age at first egg and survival. The base population was established from 3000 eggs purchased from various locations in the Horro region and these were placed at the Ethiopian Institute of Agricultural Research in Debre Zeit, Ethiopia. Twenty cockerels and 260 hens were successfully hatched and raised, and these formed the parental population. Selection was based on individual performance ('own performance' or 'mass selection') until the eighth generation. In each generation, approximately 600 males and 600 females were produced as selection candidates and recorded for body weight and egg production. Females were selected based on own performance for body weight and egg production. Males were selected based on their performance for body weight. Selection pressure was 10–20% in the males and 50–60% in the females.

Evaluation of the breeding programme was conducted when the programme was in generation 8. Breeding values were estimated for both cumulative egg numbers at 45 weeks of age and body weight at 16 weeks of age to evaluate the trend of changes over the generations. The genetic trends showed that by generation 8, survival had improved from less than 50% in the base generation to almost 100% in generation 8. Body weight per bird at 16 weeks had increased substantially from 550 g to 1100 g. Egg production tripled from 64 eggs per hen per year in the base generation to 172 eggs per hen per year by generation 8. Every generation of pure-line Horro birds was kept and used as parents for the coming generations. The nucleus flock established was kept at the Debre Zeit Agricultural Research Centre. The genetic change achieved through selection was monitored by comparing the unselected animals with the selected ones. This breeding programme achieved a large and significant improvement above unselected village chickens. While the performance of this population was lower than that of commercial chicken lines (the difference decreasing with each generation of selection), the improvement was impressive. And when adaptability, taste and likeability were taken into account, the improved indigenous birds were clearly superior to commercial chickens.

Box 1.6. Community-based sheep and goat breeding programmes.

A community-based breeding programme, implemented by the International Centre for Agricultural Research in the Dry Areas (ICARDA), ILRI, Boku University and the Ethiopian NARS, was started in 2009 in Ethiopia (ICARDA, 2018; Haile *et al.*, 2019). The programme combined selective breeding of sheep and goats based on production parameters, such as body weight, lambing rate and survival. At the time of this assessment, 3200 households in 40 villages had benefitted with an average income increase of 20% in the programme sites of Bonga, Horro and Menz. Farmers had created 35 formal breeders' cooperatives to participate in the programme, and it had been replicated in more than 40 programmes that sprang up based on inspiration and learnings from the original site. Most of the participating households in Menz no longer needed assistance from government-run safety-net programmes that provided food; they were able to use their income from sheep sales to buy food. The breeding cooperatives were able to build capital from buying rams and bucks as well as from other investments. For example, the Bonga cooperative had a capital of around US$60,000. There was a high demand to breed rams and bucks from neighbouring communities and other governmental and non-governmental programmes. The government identified the community-based breeding programme as the strategy for genetic improvement of small ruminants in the Ethiopia Master Plan and Growth and Transformation Plan II, and the programme is being replicated in Iran, Malawi, South Africa, Sudan, Tanzania and Uganda.

(iii) developing sustainable public–private partnerships for improvement, multiplication and delivery of the identified genotypes and other value chain services; and (iv) placing women at the centre of the project to ensure its success, given that women are the primary owners, managers and traders in chickens and chicken products in these countries.

Box 1.7. Red Maasai and Dorper sheep breeding programmes.

Starting with a sheep flock established in 1997 as an experimental flock comprising purebred Red Maasai and Dorper sheep and their crosses, a breeding programme was introduced in 2003 aimed at improving the growth performance and resilience of the main breeds and their crosses under range conditions. Following droughts and loss of animals by pastoral livestock keepers in 2008–2010, the ILRI flock of 1100 sheep became a main source of breeding animals for communities living within the surrounding rangelands in Kenya and neighbouring countries. Informed by the finding that many genes, each with small effects, rather than one major gene were involved in conferring resistance in the Red Maasai breed to endoparasites, ILRI established a multi-trait selection programme for both Red Maasai and Dorper × Red Maasai crosses under natural and continuous challenge, with the next-generation sires and dams identified from among the young rams and ewes selected on the basis of survival, growth rate and lambing intervals under parasite challenge. The net effect was that the Red Maasai and their crosses with Dorper sheep had, over more than 12 years of selection, improved, with their 9-month weight having almost doubled, the age at first lambing and lambing intervals having slightly decreased, and lambing rates having improved. The most important outcome of this work was that ILRI's flock at its Kapiti Ranch remained one of the two major sources of improved Red Maasai rams in Kenya, with requests far above what could be supplied. Indeed, after the prolonged drought of 2008, ILRI provided many local farmers with replacements for Red Maasai sheep. With this experience, Kapiti rams were used to initiate further Red Maasai genetic improvement under community-based set-ups in Nyando, Kisumu County, and in Trans Mara, Bomet County, Kenya. Inspired by these developments, a Red Maasai breed society was registered in the Kenya Livestock Breeders organization and supported by a collaborative project of ILRI and the African Union–Interafrican Bureau for Animal Resources (AU-IBAR).

Box 1.8. Project to identify and deliver adapted chickens for productivity.

The vision of the ACGG project was to catalyse public–private partnerships for increasing smallholder chicken production and productivity growth as a pathway out of poverty in sub-Saharan Africa, with project sites in Ethiopia, Nigeria and Tanzania, countries with substantial poultry endowments and where the needs and opportunities for enhanced chicken productivity were considered among the greatest on the continent. The project was designed on the premise that having available and affordable brooded and pre-vaccinated chicks adapted to typical low-input systems in poor rural communities would greatly increase their chicken production and productivity and would reduce poverty, especially among poor women. Ten tropically adapted, low-input but productive chicken breeds from Africa and elsewhere were tested under on-farm conditions. Chicks were pre-vaccinated and brooded to 21 days old before distribution to households. The results showed that significant productivity gains could be made by testing and promoting chicken breeds that are more productive, tropically adapted and farmer preferred. The chicken strains that ACGG made available to farmers had significantly higher productivity in terms of both live body weight (an average of 200–300% higher than indigenous types) and egg production (100–200% higher) than the local chickens raised by more than 6000 farm households involved in the project.

With the testing nearly completed in the three project countries, the project in 2020 is focusing on developing the private-sector-led institutional arrangements for delivery mechanisms that will ensure that the preferred chicken strains identified are available to smallholders at competitive prices at the village level. For example, hatcheries partnering with ACGG started multiplication and delivery at scale to smallholder farmers. At the same time, the project has begun, as a next phase, to develop a roadmap for long-term genetic gains to ensure ongoing genetic improvement of the identified breeds/types. Beyond the project countries (Ethiopia, Nigeria and Tanzania), the germplasm, data and knowledge generated have the potential to benefit millions of poor rural and peri-urban households in other countries where backyard chicken production systems dominate.

Reproductive technologies for smallholders

In Africa, only Kenya and South Africa have had active research in semen sexing and *in vitro* fertilization. ILRI's work in its facilities in Kenya has adapted and tested potential applications of selected technologies to address smallholder challenges. For example, scientists from ILRI and the Department of Clinical Studies at the University of Nairobi succeeded in producing Kenya's first test-tube calf in 2009 using a technique called *in vitro* embryo production (IVEP), which makes it possible to rapidly multiply and breed genetically superior cattle within a short generation interval. IVEP eliminates the tedious steps of synchronizing donor cows and has the advantage of maximizing utilization of appropriate dam and sire genotypes by increasing the efficiency of multiplication in breeding, permitting determination of sex of the offspring and facilitating the pre-testing of actual fertility status of the sire. IVEP can produce up to 300 offspring per lifespan of a dam. ILRI and partners have also applied the IVEP technique in combination with sexed semen in what is called fixed-time artificial insemination. These protocols and the accompanying capacity were the basis of the programme for ILRI's cloned calf (Yu *et al.*, 2016).

Domestication of fixed-time artificial insemination (FTAI) protocols have enabled synchronization and have been used to extend artificial insemination to nine counties in Kenya that were previously considered unsuitable for high-yield dairying. This extension of FTAI has produced enough cross-bred heifers to support related businesses, such as private artificial insemination, and milk bulking and chilling services, in some of these counties. The Ethiopian application of FTAI has resulted in hundreds of thousands of new dairy cross-bred cows and is currently underpinning the country's dairy improvement plan.

Although the worldwide success rate of producing live cloned offspring from high-quality domestic livestock has improved in the past two decades since the successful cloning of Dolly the sheep in 1996, little has happened in Africa in this regard. ILRI scientists have undertaken research on cloning as a tool for supporting its animal health and broader research on genetics of adaptation, specifically as part of the efforts to explore the possibility of incorporating disease resistance traits of some of Africa's indigenous breeds into more productive breeds. Through these efforts, ILRI produced the first African livestock cloned by somatic cell nuclear transfer using primary embryonic fibroblasts. The only other successful cloning in Africa was Futhi (Zulu for 'replica'), a Holstein heifer born at the Artificial Insemination Centre at Brits, North West Province in South Africa, in April 2003, through a collaboration between scientists from South Africa and Denmark. Unlike Tumaini, Futhi was derived from a single cell taken from the ear of a donor cow, inserted into an ovum and later implanted into a recipient cow. Cloning of Tumaini was a proof of concept for a technology that could be used to develop improved farm animals, carrying traits of economic importance such as disease resistance (e.g. trypanotolerance).

Strengthening NARS Capacity in Livestock Genetics

Inadequate capacity is one of the major constraints to agricultural development in most of the developing world, especially in Africa and Asia. A recent study commissioned by FAO in 2017 found that the major constraints to application of most agricultural technologies in Africa relate to inadequate human capacities, facilities, financial investments and institutional capacities. In most countries, there remains a major lack of a critical mass of scientists in areas relevant for agricultural biotechnology, especially in the more advanced areas of modern biotechnology, such as molecular biology, genomics and bioinformatics.

In the livestock sector, working in partnership with national and other international partners, ILRI has contributed substantially in the research and application of medium- to high-level biotechnologies for genetic characterization and improvement of livestock. These have been implemented through four main streams: graduate training, group training, individual short-term training and internships, and coaching and mentorship achieved through collaborative projects. These are summarized below, with special reference to animal genetics and breeding.

Capacity development

ILRI has trained many MSc and PhD students in genetics and breeding, either through fellowships or in collaboration with NARS where ILRI-hosted fellows work. Since 2004, the facilities of the Biosciences eastern and central Africa–ILRI Hub (BecA-ILRI Hub), especially the Hub's genomics and bioinformatics platforms, were a major means of delivering high-quality training, including exposure to cutting-edge research facilities and approaches. As such, many of these fellows subsequently became research leaders in their own institutions, and some have retained intensive collaboration with ILRI and other institutions internationally, with these fellows using their relationships with ILRI to develop projects and to provide opportunities for next-generation graduate fellows. Indeed, many among the current generation of leading livestock geneticists in African and, to a smaller extent, Asian NARS have connections with ILRI, with a majority of these having spent time in ILRI's laboratories. ILRI has trained an estimated 200 BSc, over 69 MSc and more than 66 PhD graduates, as well as over 35 postdoctoral fellows in livestock genetics and breeding.

Group training

Through its research programmes on cattle and small ruminants, ILCA organized, starting in mid-1980 until its merger with ILRI in 1995, annual courses for 25–30 NARS scientists in the design and analysis of livestock breeding programmes. These early courses focused on analysis and interpretation of data from on-station and on-farm breeding programmes.

ILRI-SLU project

Starting in 1999, ILRI collaborated with the Swedish University of Agricultural Sciences (SLU) on a global project, 'Capacity Building for Sustainable Use of Animal Genetic Resources in Developing Countries', using a 'training the trainers' model (Fig. 1.3). This capacity-building project directly targeted NARS scientists in developing countries who are responsible for research and training in animal breeding and genetics. The objectives of the project were: (i) to strengthen the subject knowledge and skills of NARS scientists; (ii) to strengthen their communication skills, to catalyse curriculum development and delivery; (iii) to develop computer-based training resources, to stimulate contacts, collaborations and networks; and (iv) to strengthen the human base for work on AnGR in developing countries.

During the ILRI-SLU project period (1999–2010), 195 scientists from 46 countries in Africa and Asia were trained in animal breeding and genetics, including in design and implementation of breeding strategies, and in teaching and communication (Table 1.1) (Ojango *et al.*, 2011).

In addition, the ILRI-SLU project developed an electronic Animal Genetics Training Resource (AGTR; http://agtr.ilri.cgiar.org; accessed 28 January 2020), which is available online and on CD. The first version of this course was produced in 2003, a second one in 2006, and an updated and expanded one (version 3) in 2011 on a fully web-enabled platform, which allows direct online revisions of content. AGTR is a unique, 'one-stop', user-friendly, and interactive multimedia resource targeted at researchers and scientists teaching and supervising postgraduate students in animal breeding and genetics. It is a dynamic training resource designed to inform the design and implementation of breeding programmes and to provide information that empowers countries and institutions to undertake their own research applying the best available information and knowledge. The AGTR course covers established and rapidly developing areas, such as genetics-based technologies and their applications in livestock breeding programmes. AGTR is essentially a platform that extends the capacity strengthening work done by the ILRI-SLU project to reach more people over a long-lasting period.

One of the objectives of the project was to stimulate knowledge sharing and networks within regions. By linking NARS and university lecturers from different countries in the training courses, three virtual regional networks were subsequently established: (i) Afrib Breeders in Africa; (ii) IAGRA in South-east Asia; and (iii) the South Asia Genetics Group. These animal breeding and genetics virtual networks were created by the project participants as tools for sharing knowledge and information and for facilitating the development and review of collaborative proposals

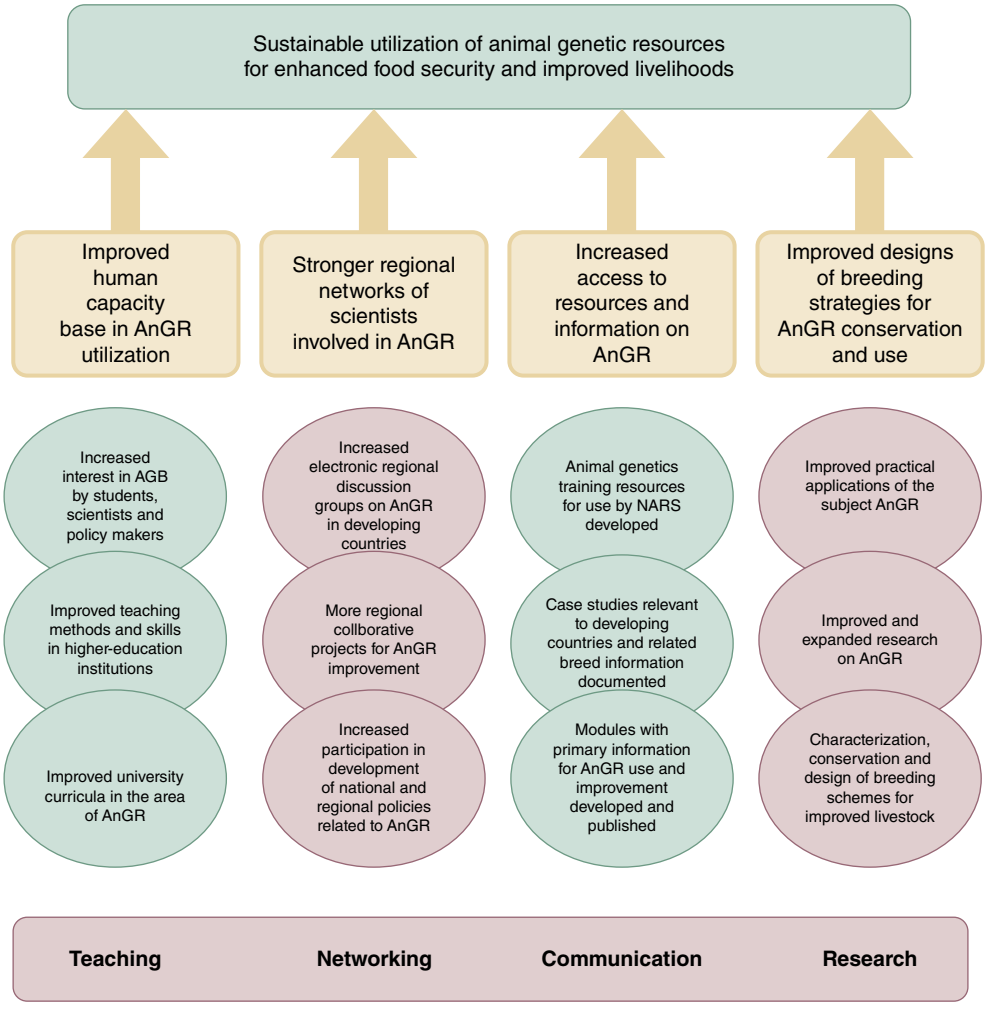

Fig. 1. 3. Outcomes of the ILRI-SLU capacity development project. (Data from ILRI archives.)

Table 1.1. ILRI-SLU training courses and trainees between 2000 and 2010. (Data from ILRI archives.)

Year	Region	Countries	Number of participants
2000	East and southern Africa	10	20
2001	West and Central Africa	10	18
2003	South-east Asia	9	18
2003	Sub-Saharan Africa	18	20
2005	South-east Asia	9	18
2006	South Asia	6	20
2006	Training request by ASARECA	9	19
2007	West and Central Africa	9	20
2008	East and Southern Africa	14	23
2009	South Asia	6	19

ASARECA, Association for Strengthening Agricultural Research in Eastern and Central Africa.

on the characterization, conservation and design of livestock breeding programmes. In this way, the project has helped to create 'communities of practice' in these regions.

ILRI has organized and delivered many short-term group training courses in genetics, genomics, bioinformatics and animal breeding, some in collaboration with the BecA-ILRI Hub platform team. For example, between 2008 and 2018, ILRI scientists provided 2-week trainings every year in a European master's degree programme in animal genetics and breeding that focused on practical applications in developing countries. The programme initially supported students from developing countries to study in Europe, after which they would return to implement their learnings in their home countries. The ILRI genetics team is a key resource for these training courses, providing topics for internships and MSc thesis co-supervision, and hosting students during their internships/MSc thesis projects. Other courses involving ILRI's genetics team include collaboration with Scotland's Rural College, which since 2014 has been running a 1-week annual training course for 21 African scientists from 14 different countries in quantitative genetics and genomic selection.

Through 'technical associates' and 'research fellows' mechanisms, ILRI's livestock genetics team has trained a large number of scientists from universities and national agricultural research institutions. Technical associates are technicians or scientific staff from NARS and other ILRI partner institutes who come to ILRI for up to 6 months for individual training at the request of their employers; this category is oriented towards persons already involved in research activities associated with ILRI. Research fellows are university and national agricultural research institution scientists undertaking work in research areas similar to those at ILRI. Designed to benefit the future research capability of the individuals and their home institutions, research fellows spend a maximum of 18 months at ILRI to undertake non-degree-related training in research methodologies, to discuss the design and planning of collaborative research, and to analyse and write up research results. While all areas of the livestock genetics programme have undertaken individual training through these mechanisms, the animal genetic characterization (phenotypic and molecular) team has hosted the largest numbers, with operationalization of the BecA-ILRI Hub platform in the early-2000s being a major driver; large numbers of scientists from across Africa sought space to extract and analyse DNA samples and to get help with their data analyses. The major constraint to ILRI's hosting even larger numbers of technical associates and research fellows has been inadequate financial resources to support them.

ILRI's livestock genetics activities have been dependent on strong partnerships with NARS, both as providers/owners of samples and data and as direct collaborators in the research process, design, experimentation, analysis and reporting of research results. These collaborations have been critical for mutual learning, with ILRI scientists benefiting by deepening their own understanding of the relevant livestock production systems and institutional contexts of research in NARS. NARS scientists, on the other hand, have benefitted from exposure to advanced research facilities and methods that many of them have no access to in their home institutions. Very importantly, the exposure has allowed many of these scientists to engage in expanded and productive networks of scientists, both in their own regions (Africa and Asia) and internationally – especially with ILRI's many traditional advanced research institute partners. Through the direct coaching of these scientists in the research process and their exposure to, and mentorship by, the ILRI research community, as well as the expanded networks they can engage in, ILRI has created a large number of global leaders in livestock genetics for development in Africa and Asia.

Conclusions and the Future

The efforts of ILRI and its partners in breed surveys, phenotypic and molecular characterization, breed evaluation studies, genetics of disease resistance, genetic improvement strategies, development of associated tools and approaches, and the wider promotion and use of these tools have collectively contributed to a deeper understanding of African and Asian livestock populations. The associated capacity development efforts have helped to broaden the application of these results and tools both in space and in time. Taken together, these investments have led to:

(i) classification and characterization of indigenous livestock breeds of Africa and Asia, using phenotypic and molecular genetic information, facilitating a greater understanding of the underlying genetic diversity in these regions; (ii) databases on the geographical distribution and physical and performance characteristics of indigenous livestock; (iii) contribution to the reconstruction of genetic history and geography, with links to human migration and settlement; (iv) confirmation of the uniqueness of specific indigenous breeds and better quantification of their unexploited potential such as disease resistance; (v) development and testing of tools for genetic characterization and conservation; and (vi) targeted application of functional genomics. Recent and exciting findings include a study on the genome landscape of African livestock (Kim *et al.*, 2017) and the development of harmonized phenotypic and genetic characterization tools and protocols led by AU-IBAR for national and regional gene banks (www.au-ibar.org/angr/432-regional-inception-workshops-for-animal-genetic-resources; accessed 28 January 2020).

The future of ILRI's genetics research and development programmes will be influenced by four factors: (i) the CGIAR global livestock agenda; (ii) ILRI's long-term strategy; (iii) emerging and anticipated livestock challenges in coming years including new infections and disease variants spreading to new regions largely driven by climate change, challenges associated with smallholder intensification, and challenges imposed by the ever-decreasing farmland and limited forage resources, requiring more feed-efficient livestock; and (iv) partnership arrangements that will require constant re-examination of ILRI's comparative advantage.

ILRI currently has a rich resource base, collaborative arrangements and a wide-scale partnership model to push its livestock genetics agenda to higher levels and with greater impacts. These include the suites of techniques, protocols and approaches for genetic improvement of livestock as discussed in this chapter, proven breeding technologies such as cloning and associated embryo transfer technologies, and other tools needed to navigate new areas of livestock improvement such as developing transgenic animals with resistance/tolerance attributes. These tools, together with global advancements in genetic technologies, including SNPs and gene drives as well as ICT platforms that can be used to facilitate the creation of integrated large-scale data systems, especially genomic data (and which can enhance the democratization of data to ensure unconstrained access by NARS), promise new possibilities for livestock improvement in the developing world.

In supporting the application of economic valuation methodologies, ILRI's work will focus on understanding and applying the economics of conservation and use in decision-making contexts such as choice of traits and breeds/genotypes, public willingness to pay for services (breeding and conservation) and incentive mechanisms for conservation. ILRI's work in this domain (e.g. Muigai *et al.*, 2009; Tarekegn *et al.*, 2016) has demonstrated the link between knowledge of genetic diversity and conservation and use programmes. In future, a more compelling link will need to be demonstrated, with practical examples across different species.

ILRI will need to explore partnerships with the private sector (the development of ICT-based platforms, such as that envisaged in the ADGG project, can provide proof of concept) while ensuring that the interests of smallholders are not compromised. Development of models for facilitating the testing and delivery of appropriate genotypes for smallholders and for ensuring ongoing genetic gains – such as what was piloted in the DGEA and envisaged in the ACGG projects – are examples. Indeed, ILRI has already shown increased involvement in on-farm breeding programmes and extension services in some countries in Africa and Asia, following enhanced partnership with NARS. It is envisaged that these endeavours will be pursued by an expanding network of global collaborators.

Note

[1]Sam Okantah, from Ghana; Wilson Mwenya, from Zambia; and Ed Rege, from Kenya.

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