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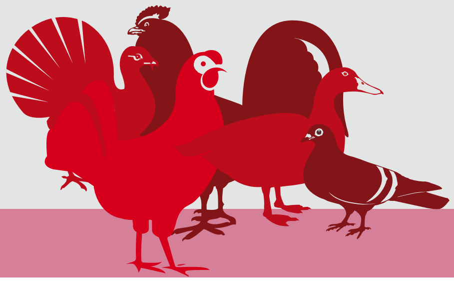
Smallholder Poultry Production

CHICKEN GENETIC RESOURCES USED IN SMALLHOLDER PRODUCTION SYSTEMS AND OPPORTUNITIES FOR THEIR DEVELOPMENT



CHICKEN GENETIC RESOURCES USED IN SMALLHOLDER PRODUCTION SYSTEMS AND OPPORTUNITIES FOR THEIR DEVELOPMENT

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Poul Sørensen has many years of experience with poultry research. His particular interest is in breeding and genetics. He has contributed to the development of Danish poultry breeding since the beginning of his career and over time came to be the leading person in this area. With the intensification of poultry breeding world-wide he shifted his attention to the consequences of narrowing the biodiversity/variation among the poultry breeds available for production. His research in the later years has been directed towards the negative side effects of ongoing strong selection for higher egg production in laying stock, and higher growth rate in broiler chickens. Since 1995 Poul Sørensen has participated as specialist on short term missions to Bangladesh and several countries in Africa Since 1997 he is a member of the directory board of " Network for Smallholder Poultry Development" KVL, Copenhagen, and has taught and supervised the 2 years MSc program "Poultry Production and Health" for 30 students from 11 developing countries.

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Keywords

Local Chicken, Major Genes, Brooding, Genetic resources, Genetic resistance, Breeding programmes

Contents

Preface

This paper is part of a series describing the opportunities and limitations of smallholder poultry production. The major structural changes that have occurred in poultry production and marketing in recent decades have lead to a strong and internationally integrated poultry industry. In developing countries, however, the majority of poultry are still kept by smallholders in less intensive systems. The advantages of these systems are the low levels of inputs that they require and the unique products they produce. These systems are practiced by people who have few other options and it is important that they persist as long as they are needed for social reasons, food security and livelihood support.

The paper describes poultry populations that are being used by smallholder farmers in developing countries. In addition to performance data of many local breeds, information is provided about the situation of these populations and analysis why they have not improved by looking at background factors like genetic disease resistance, major genes, brooding capacity, biodiversity, genotype by environment interaction, preferences for free range local chickens and the progress in use of molecular genetics. The literature review includes information from peer reviewed journals as well as PhD and MSc theses that were prepared during an education programme that was supervised by the author. The paper concludes with reflections on what would be lost if these populations disappear and possible strategies to improve these populations.

We hope this report will provide accurate and useful information to its readers and any feedback is welcomed by the author and the Animal Production Service (AGAP)[1] of the Food and Agriculture Organization of the United Nations (FAO).

[1] For more information visit the FAO poultry website at: http://www.fao.org/ag/againfo/themes/en/infpd/home.html or contact: Olaf Thieme – Livestock Development Officer – Email: olaf.thieme@fao.org
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Chicken genetic resources used in smallholder production systems and opportunities for their development

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SUMMARY

The paper offers an overview of current knowledge regarding the chicken genetic resources kept in smallholder production systems in developing countries. FAO has classified poultry production into four sectors: sectors 1 and 2 comprise large-scale commercial operations; sector 3 comprises small-scale commercial farms; sector 4 comprises backyard and scavenging production, and is largely based on indigenous birds, often belonging to local breeds that have been kept for many years in a particular area and are adapted to local conditions. In a large numbers of developing countries in Africa and Asia, indigenous birds constitute up to 80 percent of the standing poultry population.

Results from recent performance trials of chickens under station and field conditions in several countries are reviewed and summarized. They show the strong influence of management conditions and indicate higher performance than in an earlier review. The ability of broodiness and for natural incubation is an important characteristic of indigenous hens. The drawback of natural incubation is the difficulty to produce large numbers of chicks at the same time – for which the rice husk incubators might be ideal.

A considerable number of genes are known to exert resistance to disease but much remains unknown. Stocks raised for many generations in a given area can be expected to show adaptive genetic resistance to the infections prevailing in the area. However, this may not protect them sufficiently if they are moved to other environments. There are a number of genes with major effects on the phenotype that seem to be of special interest for poultry keeping in smallholder systems in developing countries. The major genes causing reduced feathering and reduced body size may improve growth capacity, but perhaps not until a late phase of growth. The naked-neck gene has a greater effect than the frizzling gene. The dwarf gene (or genes) reduces body size and the length of the long bones.

Further understanding of the genetic characteristics of indigenous poultry populations is expected through characterization of genotypes by molecular methods but the advantages

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of indigenous chickens are not only determined by production characteristics but also by consumer preferences and cultural factors.

Option for genetic improvement of indigenous chickens through crossbreeding and experiences from countries are presented. The experience of the Bangladesh model shows the difficulties involved in implementing such a crossbreeding programme in a low-input system. The Fayoumi breed in Egypt is a rare example of a breeding programme for local chickens in a developing country. Local breeds have been shown to possess both superior levels of genetic variation relative to commercial breeds and unique phenotypic traits signifying valuable local adaptations. Assuming the low input/output smallholder system will continue to exist in many parts of the developing world, sustainable progress in productivity of 2–4 percent per year will be possible using local chickens.

1. INTRODUCTION

Outbreaks of highly pathogenic avian influenza (HPAI) in Asia and later in Africa, and the search for effective disease control measures, have focused attention on small-scale-poultry production systems. Sectors 3 and possibly 4 are said to be particularly in need of restructuring although quantification of the relative importance of these sectors to the spread of the disease is difficult. The Options for restructuring need to be assessed in the light of a thorough understanding of village poultry production systems and their contribution to income generation, food security, rural development and the sustainable use of poultry genetic resources.

Smallholder poultry production makes use of local or indigenous genetic resources, which differ from commercially bred poultry in several respects:

- The birds are adapted to a harsh environment where resources are often limited and where challenges imposed by climatic conditions, pathogens and predators are severe.
- They are often utilized for several purposes simultaneously, and therefore may outperform specialized commercial breeds when scored for multipurpose productivity.
- Many indigenous poultry breeds have been isolated from planned breeding and genetic divergence is potentially high.

Devising a successful plan to improve or restructure some of the smallholder poultry production systems requires that all the above points are given due consideration when comparing local and exotic breeds. When the goal involves genetic improvement of local breeds, it is also important to consider the following:

- Exotic breeds that are considered candidates for improvement of local stock should be evaluated under realistic management conditions that resemble the reality of smallholder farming.
- Cross-breeding programmes based on hybrid production require careful planning of the logistics involved in breeding and distributing hybrid poultry to smallholders. The sustainability of such programmes should be critically evaluated before they are initiated.
- Genetic improvement by introgression of genes from exotic breeds into local stock requires careful evaluation of the optimal input of foreign genes needed to improve production traits without disrupting the local adaptation of the indigenous breeds.

Again, it is crucial that testing is done under realistic farming conditions.

- The alternative to introducing exotic genes is a breeding programme focused directly on local breeds. Such programmes require an adequate framework for offspring testing under realistic conditions, and the presence of sufficient genetic variation for production traits.

The papers is structured as follows: a first section describing the performance of indigenous breeds – including subsections on brooding and natural incubation, genetic resistance to diseases, major genes and the potential for using molecular methods to characterize the genotype; a short section on preferences for free-range local chickens; a third and larger section on how to introduce genetic improvement under smallholder conditions, which covers performance comparisons of cross-bred local × exotic birds, genotype by environmental interactions and breeding programmes; and a section on conservation and biodiversity, which describes the status of poultry genetic resources and the tools available for conservation. Finally, some recommendations for the future are offered.

The work is based on published literature and secondary information; it focuses primarily on chicken production, as this is the largest and best documented area of smallholder poultry production. Examples from ducks, geese and guinea fowl are included where relevant material exists.

2. PERFORMANCE OF INDIGENOUS BREEDS AND ECOTYPES OF CHICKENS

An initial question should be: what information is needed to quantify the performance of local chickens? In Africa, chicken meat is often of primary interest; the main focus will therefore be on body weight at market age. However, it is also important to know the reproductive capacity. If natural incubation is used, the number of chickens raised per mother hen needs to be considered. If artificial incubation is used, the number of eggs laid is of primary interest. In Asia and South America, eggs are the main marketed product of local chickens; egg production capacity is therefore of major interest – followed by meat production capacity.

There are vast amounts of data on the performance of local chickens from tropical zones, but often they are not directly comparable, as the way in which information is gathered varies from study to study. Most studies can be classified according to the schema outlined in Table 1.

There is often a big difference between results obtained from a research station, where the cost of feed is not a problem, and those obtained from field systems in rural areas, where the farmer may be unwilling or unable to meet the cost of supplying feed for the birds. The result of a station test reflects the genetic capacity of the tested breed, while a field test provides a more realistic measure of performance under the prevailing production conditions. Station tests often involve birds being kept in cages and allowed free access to feed; the focus is on body weight and egg-laying capacity. Field studies are often based on semi-scavenging feeding systems, with various degrees of information being made available about the use of supplementary feed. It is also important to know whether the hens from which egg production data are recorded are also used for incubation/brooding (see section on brooding, below). Finally, it is essential to know the method by which the data have been obtained – direct data recording or questionnaire survey?

TABLE 1
Classification of performance studies

Aspect of the study	Alternatives		
Management	**Research station**	**Field**	
Feeding level	Free access to concentrates	Semi-scavenging	Scavenging
Product orientation	Egg production	Brooding/meat	
Information system	Questionnaire	Recording over a period of time	

Horst (1988) presented a table of performance studies of native chickens from all tropical regions. The data were categorized according to whether they were from station or field studies. The following paragraphs present an overview of information that has appeared since Horst's study was compiled; conclusions are drawn based on the Horst data and those from the later studies.

Islamic Republic of Iran

Two reports from the Islamic Republic of Iran provide information on the egg production capacity of the local breed known as the Isfahan Native Fowl. The first report (Ansari, 2000a) describes a study that compared the original unselected breed to an improved version (selected for faster growth and better egg production). During two consecutive generations, hens were distributed to farmers at eight weeks of age and kept under rural conditions until they were 66 weeks old. The birds were not used for incubation during this time. The second report (Ansari, 2000b) describes the production capacities of the same populations under station conditions. The results of these studies are summarized in Table 2.

TABLE 2
Productivity of the Isfahan breed in the Islamic Republic of Iran

	Field data to 66 weeks of age			Station test: 32 weeks	
	Rate of lay (%)	**Age at first eggs (weeks)**	**Egg weight (grams)**	**Rate of lay (%)**	**Body weight at 8 weeks**
Unselected hens (generation 1)	27.4	26.0	50.5	64.0	764
Unselected hens (generation 2)	37.5	26.0	45.8		
Selected hens (generation 1)	26.4	25.4	51.7	70.3	748
Selected hens (generation 2)	43.8	27.2	45.8		

Sources: Ansari (2000a and 200b).

Thailand

Thai indigenous chickens (TIC) are kept by about 6 million households (Choprakarn, 2007). Flocks consist of three to five hens and a cock. The birds exist on scavenging and household leftovers. A hen produces 35 eggs per year in 3.5 clutches, resulting in 20 to 25 day-old chicks. A chick mortality rate of 70 percent leaves six to eight chickens per hen per year to be marketed. TICs are relatively resistant to common poultry diseases like Newcastle disease, fowl cholera and fowl pox, and survive at a higher rate than exotic breeds and their crosses.

Viet Nam

The Ri chicken is a local breed in northern Viet Nam. Recently, the Tamhoang breed from China, which is bred as a dual-purpose bird, has been imported into the area (Minh *et al*., 2004). Farmers in northern Viet Nam provide supplemental feeds for their chickens during periods where surplus grain is available. This prompted the authors to investigate the performance of the two breeds under different levels of supplemental feeding (ibid.). After three months of laying, hens of the two breeds were distributed among eight farmers. Within the farms, hens were assigned to four different levels of feeding: free access; 60 grams maize; 24 grams soybean; or 54 grams mixed feed per bird per day. Over 14 weeks, the hen-day egg production rate of the Tamhoang breed was 24.4 percent – significantly higher than the 16.7 percent of the Ri breed. The hens on mixed feed had the highest egg production rate (22.8 percent), while the 24 gram soybean group had the poorest (17.7 percent). The feed cost per kg of egg was almost twice as high for the free access group as for the three other groups. Feed cost per kg of eggs averaged across the four treatments was US$1.2 for the Ri breed and US$1 for the Tamhoang breed. The authors conclude that the Chinese Tamhoang is the most suitable breed for the semi-scavenging systems if the birds are supplied with the quantity and quality of supplements used in the experiment.

Khanh (2004) compared birds from four indigenous Vietnamese breeds kept at the National Institute of Animal Husbandry in Hanoi. The birds were kept under station conditions, on the floor, and with free access to feed. The production figures obtained are shown in Table 3.

TABLE 3
On-station production parameters of four local breeds from northern Viet Nam

Breed	At 16 weeks		Egg production in 8 months		Age at first egg (weeks)	Hatchability (%)
	Weight (kg)	Kg gain per kg feed	Rate of lay (%)	Numbers		
Ac	768	0.15	26.8	63	16.9	66.7
H'Mong	1 172	0.15	32.9	72	19.5	68.3
Mia	2 124	0.33	37.5	74	22.5	73.0
Ri	1 263	0.14	43.0	94	19.5	84.6

The birds had free access to feed.
Source: Khanh (2004).

The results indicate that for meat production the Mia breed is the best choice, in particular because the feed conversion efficiency is about twice as good as that of the other breeds at 16 weeks. The growth curve of the Mia is interesting, as the birds grow slowly (like the other breeds) until they are eight weeks old, after which the growth rate increases (24.5 grams/day vs. 13.5 grams/day). The other breeds have a daily gain of 11grams/day throughout the whole period. The Ri breed is the most widely used indigenous breed in Viet Nam. This seems to be the right choice if egg production is the major objective. The Mia breed, conversely, might be of particular interest for organic broiler production as practised in Europe. According to the rules for organic production, the broilers have to grow for at least 14 weeks before slaughter. Under such a system, the growth pattern of the Mia would minimize the use of feed to meet the maintenance requirements of the birds.

India

In India, the Kadaknath breed of the Jhabua District of Madhya Pradesh is known to be well adapted to the harsh environment, which is characterized by extreme climatic conditions and poor management, housing and feeding. Because, long ago, the Kadaknath breed was reared by tribal people, and following many years of selection mainly for plumage characteristics, there are three varieties: Jet Black; Pencilled; and Golden Kadaknath (Thakur *et al*., 2006). A recent study of their growth potential recorded a daily weight gain of 6.2 grams from 0 to 20 weeks of age – based on growth in the breed's usual production environment, with very little supplemental feed (ibid.). An egg-quality study (Parmar *et al*., 2006) showed that Kadaknath hens lay brown-shelled eggs weighing 43 grams, with a yolk proportion of 34 percent and a shell thickness of 0.31 mm. No information on pure-bred egg production has been reported.

In the islands of the Bay of Bengal, a local poultry breed known as the Nicobari is well adapted to the tropical climate and survives and produces well compared to exotic populations. A study by Sunder *et al*. (2005) compared three groups of Nicobari hens and a White Leghorn adapted to the local climate. The birds were kept for a year in individual cages and fed with a standard mixture. The results are shown in Table 4.

TABLE 4
On-station production levels of Nicobari hens and a strain of White Leghorn

	White Nicobari	Black Nicobari	Brown Nicobari	White Leghorn
Age at first egg (weeks)	24.9[ab]	25.6[b]	26.6[b]	21.64[a]
Annual egg production	165.2[b]	155.3[ab]	142.2[a]	186.2[c]
Rate of lay (%)	48.9[b]	46.7[ab]	43.6[a]	51.6[c]
Weight at 20 weeks (kg)	1.055[a]	1.183[c]	1.127[bc]	1.086[b]
Egg weight (grams)	48.2[a]	49.8[a]	46.7[a]	51.2[a]

Birds were kept in individual cages.
Means within a row with no common superscript differ significantly (P<0.05).
Source: Sunder *et al.* (2005).

Bangladesh

The so-called Deshi chickens of Bangladesh constitute about 90 percent of the indigenous chickens in the country, and therefore number about 130 million birds. They are the chickens most commonly raised by the many smallholder farmers who keep flocks of five to six hens. Bhuiyan *et al*. (2005) report that Deshi hens have a daily weight gain of 3.5 grams to 12 weeks of age and a mature weight of 1.1 kg. They produce 48 eggs per year, distributed over 3.5 clutches.

Morocco

In Morocco, Benabdeljelil *et al*. (2001) surveyed 106 households in three villages to obtain production parameters for the local chickens known as Beldi. The birds were kept under semi-scavenging conditions in small flocks – about five hens and one cock as the reproducing unit. The Beldi breed is obviously derived from a variety of Mediterranean breeds introduced by invaders. It has several of the characteristics of Mediterranean breeds, such as large single comb and prominent white earlobes; it therefore seems to be different from typical African breeds (ibid.). In spite of the growth in the industrial poultry sector, rural poultry remains a steady supplier of highly appreciated products for the consumer. Performance information obtained from farmers through interviews is shown in Table 5.

Egypt

The well-known Fayoumi breed has been used for many years in the Fayoum Governorate of Middle Egypt. It was probably derived from the Silver Campine breed during the early nineteenth century. The Fayoum Poultry Research Station was established during the mid-twentieth century. In 1958, the Fayoum Poultry Cooperative Society was established for the purpose of distributing the chickens to farmers and smallholders (Hossary and Galal, 1994). The breed has been transferred to several countries; the best described case is the use of the Fayoumi and the Rhode Island Red to produce cross-bred birds in Bangladesh

TABLE 5
Performance of chickens raised in rural condition in Morocco

Trait	No of farmers	Average	Minimum	Maximum
Age at first eggs (weeks)	61	29.0	17	43
Length of laying series (days)	61	28.9	14.5	60.0
Number of clutches per year	50	3.0	1	5
Clutch size (number)	60	13.5	7	18
Hatchability (% of eggs set)	60	71.0	30	100
Number of eggs per year	52	78.0	49	150
Rate of lay (%)	52	21.3	13.4	41.1

Data obtained by questionnaire.
Benabdeljelil *et al.* (2001).

TABLE 6
Production performance of Fayoumi hens obtained in Egypt under station-like conditions

Trait	Line GG	Line PP	Line "1958"
Daily gain in females (grams)	9.0	7.9	5.9
Body weight at 12 month for females (grams)	1 671	1 456	1 120
Egg weight at 12 months (grams)	47	46	45
Age at 1st eggs (days)	203	172	188
Rate of lay to 72 weeks (%)	60.8	65.1	42.4
Fertility (%)	96	95	87
Hatchability (%)	88	89	77

Line GG and PP are contemporary from 1992, while the Line 1958 refers to data for the unselected Fayoumi at the station from 1958.
Source: Hossary and Galal (1994).

(Rahman *et al.*, 1997). Hossary and Galal (1994) present performance figures for two lines of Fayoumi kept in station-like conditions and selected for some years either for higher eight-week body weight (Line GG) or for higher egg number (Line PP); these are compared to the production levels in 1958. Table 6 shows the data.

It is not clear which types of Fayoumi have been distributed to the various part of the world, but body weight figures indicate that it is mainly the PP line. The Fayoumi is generally known to have good disease resistance. Studies on infection with coccidiosis have shown that Fayoumi birds survive considerably better than White Leghorn, Rhode Island Red or Mandarah (another Egyptian breed) (Hamet and Mérat, 1982; Pinard van der Laan *et al.*, 1998). Conversely, the Fayoumi has proven to be more susceptible to Gumboro (infectious bursal disease or IBD) (Anjum *et al.*, 1993; Hassan *et al.* 2002). This supports the view that resistance to a specific infection will sometimes be accompanied by susceptibility to another.

Senegal

Local chickens in central and southern parts of Senegal were characterized by Missohou *et al.* (1998). Fifteen different plumage colours were identified, with brown and white being the dominant colours. The majority had normal feather cover, with rather few being naked neck-type birds. Adult body weight for hens was 1.3 kg. They were recorded to lay 60 eggs per year (rate of lay of 16.4 percent), with an egg weight of 31 grams. The majority of eggs are used for brooding.

Kenya

Njenga (2005) provides a productivity assessment of indigenous rural hens from Kenya. The study comprised an experimental on-station element and a field assessment based on interviews with farmers. The experimental part of the study involved collecting 128 local hens and 21 local cocks from four different eco-zones in coastal Kenya, which were then tested on a government station. Data were collected for half a year from birds with either

TABLE 7
Performance of local hens in coastal Kenya

	Station		Field
	Normal feathered	special phenotype (Naked neck, frizzling, dwarf	
Mature weight, (kg)	1.3	1.3	-
Rate of lay (%)	23.0	32.0	11.4*
Egg weight (grams)	42.5	42.2	-
Hatchability (%)	78.5	72.8	84.6

*Based on clutch size and numbers of clutch per year. The hens may have produced additional eggs that were used for consumption.
Station data based on half a year of production; data are collected per pen. Field data are based on interviews with farmers.
Source: Njenga (2005).

normal or special phenotypes (naked neck, frizzling and dwarf). The data obtained through interviews with farmers provided information on performance under semi-scavenging/brooding conditions for chickens from the same populations. The performance data for both systems and phenotypes are shown in Table 7.

Nigeria

In Nigeria, 80 percent of hens belong to local breeds (Fayeye *et al*., 2005). A study of the Fulani ecotype, native to the dry part of Nigeria, indicated that the egg shell, in particular, seems to be of higher quality than that recorded in most other studies worldwide (ibid.); the percentage of shell was 12.8 percent of 40 gram eggs and the shell thickness was 0.58 mm – comparing favourably to the 9 percent and 0.35 mm observed in most European random sample tests. Thus the Fulani breed might be of particular interest to conserve for the future.

In a study based on interviews with 100 farmers keeping local chickens in Ogun State, Nigeria, Dipeolu *et al*. (1996) found that the native hens produced only seven eggs per clutch under semi-scavenging conditions, with an average of 3.23 clutches per year – amounting to 22.6 eggs per hen per year. Ibe (1990) claims that local hens under extensive conditions lay 60 to 80 eggs per year, which increases to 124 eggs when birds are kept in battery cages.

Tunisia

Bessadok *et al.* (2003) reports that fertile eggs were collected from typical local birds in eastern Tunisia. After hatching and rearing, the hens produced were monitored for egg production under station conditions; 127 eggs were obtained over a one-year laying period.

United Republic of Tanzania

A study in the United Republic of Tanzania investigated the productivity of local chickens under rural conditions in six villages in the Morogoro District (Mwalusanya *et al*., 2001).

Eight families per village were involved over a period of nine months. The farmers were given data sheets to record the production of tagged chicks. All birds were weighed during monthly visits. The mean flock size was 16.2 birds. Their productivity is shown in Table 8. Also in the United Republic of Tanzania, Msoffe *et al*. (2004) identified and investigated seven ecotypes. The parental birds were purchased from villages on the Tanzanian mainland and islands, such that seven different ecotypes were identified. Twenty hens per ecotype, with a history of producing between one and three clutches, and three to four cocks were transferred to a station where they were kept, on deep litter, separated by ecotype, and fed

TABLE 8
Productivity of local chickens kept under field conditions in Morogoro, United Republic of Tanzania

Variable	Average	Range
Eggs per clutch	11.8	6–28
Clutches per year	2.68	
Eggs per hen per year	31.6	
Egg weight (grams)	44.1	32–57
Hatchability (%)	83.6	30–100
Growth rate (grams/day to 10 weeks)	5.4 (males) 4.6 (females)	2.1–9.1 (males) 1.2–7.0 (females)
Growth rate (grams/day 10–14 weeks)	10.2 (males) 8.4 (females)	5.3–14.7 (males) 5.5–11.1 (females)
Survival rate to 10 weeks of age (%)	59.7	11.1–100

Data based on close contact with 48 farmers.
Source: Mwalusanya *et al.* (2001).

TABLE 9
On-station productivity measures for seven Tanzanian ecotypes kept under station conditions

Ecotype	Fertility (%)	Hatchability (%)	Egg size (grams)	Daily gain 0–20 weeks (grams)	
				Male	Female
1	70^{bc}	55^{a}	37.2^{a}	5.6^{a}	4.2^{a}
2	75^{bc}	57^{a}	41.1^{b}	7.6^{bc}	5.2^{bc}
3	69^{bc}	64^{ab}	49.3^{e}	7.5^{bc}	5.5^{c}
4	64^{a}	55^{a}	42.6^{d}	8.8^{d}	6.1^{d}
5	64^{a}	74^{b}	41.9^{c}	7.4^{b}	5.4^{c}
6	68^{bc}	63^{ab}	43.0^{d}	8.7^{d}	5.9^{d}
7	80^{c}	66^{ab}	42.6^{d}	8.2^{c}	5.0^{b}

Means within a column with no common superscript differ significantly ($P<0.05$).
Incubation was in artificial incubators. Fertility was percentage of fertile eggs at 7 days and hatchability was percentage of chicken from fertile eggs.
Source: Msoffe *et al.* (2004).

ad lib. Results are shown in Table 9. Hatchability rates under artificial incubation were low (compared to the 84 percent from natural incubation). Given that in its normal production environment the breed is reproduced through natural incubation, this may indicate that artificial incubation requires some sort of genetic adaptation.

Malawi

In Malawi, Gondwe and Wollny (2005) compared the growth potential of local chickens from the southern part of the country to 20 weeks of age. One or two chickens from each clutch were collected from farmers in the study area at the age of eight weeks; the birds were then kept in cages and fed a maize and soy-based ration. The results are presented in Table 10.

The chickens kept under optimal conditions had a 40 percent better daily gain when kept in cages and given typical broiler diets, but this still is far below the capacity of commercial broilers. Safalaoh (1997) reports that the indigenous chickens raised in the rural areas of Malawi start laying at 22 weeks of age, have a body size of 1 376 grams and have a great variety of plumage colours.

The Black Australorp (BA) has often been used in Malawi as an exotic breed intended to improve the output of free-range chicken production in rural areas. In the middle zone of Malawi, Gondwe and Wollny (2003) provided farmers who had experience in raising local chickens with three nine-week old BA chickens and a number of local chickens (LC) of about the same age. These chickens (in total 125 BA and 124 LC) were raised as free-range scavenging chickens supplemented with household leftovers. In addition, 64 BA chickens were raised under station conditions. Body weights at 20 weeks were 1 090 grams, 1 000 grams and 920 grams, respectively, for BA at the station, LC in the fields and BA in fields; i.e. there was hardly any difference.

Ethiopia

Tadelle *et al*., (2003) investigated the village chicken production system in five different zones in Ethiopia. By integrating a structured questionnaire with participatory rural appraisal and a recall survey to establish specific performance history for each hen, they obtained a detailed and very reliable data set for reproductive performance. The findings are summarized in the Table 11. The results indicated no differences among the various regions.

With respect to meat production, data from Ethiopia are scarce. Tadelle *et al*. (2000) refer to some local reports that compared White Leghorn hens with indigenous hens, and

TABLE 10
Performance of local chickens in southern Malawi

	Birds kept in cages	Birds kept under semi-scavenging conditions
Weight at 20 weeks (grams)	1 077	848
Daily gain 8–20 weeks (grams/day)	10.6	7.5

Source: Gondwe and Wollny (2005).

TABLE 11
Performance of local hens under village conditions in five regions in Ethiopia

Trait	Study region					Overall mean
	Tilili	Horro	Chefe	Jarso	Tepi	
Age at first egg (weeks)	29.9	29.0	29.5	29.5	29.9	29.6
Eggs per hen per year[1]	47.1	44.4	45.8	47.3	46.3	46.4
Eggs per hen per year[2]	72.0	75.6	73.1	76.0	75.0	74.6
Rate of lay (%)[1]	19.7	20.7	20.0	20.8	20.5	20.4
Number of clutches per year	2.2	2.0	2.3	2.1	2.0	2.1
Eggs per clutch[3]	14.7[a]	13.2[b]	14.5[a]	12.8[b]	12.3[b]	13.5
Hatched chicks (%)	64.6	68.2	67.6	71.1	72.3	68.9
Survived chicks at 8 weeks (%)	52.6	47.7	53.0	57.1	49.4	51.6

[1] For hens used for incubation.
[2] For hens not used for incubation.
[3] Means in a row with no common superscript differ significantly ($P<0.05$).
Source: Tadelle *et al.* (2003).

found that the local female chickens weighed 61 percent and local males 85 percent, of the weight of a White Leghorn. However, the dressing percentage was higher for the local birds.

Bolivia

From Bolivia, there is a report on the local hens from two villages in the Chuquisaca Department in the southern part of the country, which is a typical agricultural area where peasants depending on subsistence farming, and is situated at an altitude of 3 200 to 4 500 m (Altamirano, 2005). Many of these farmers have a few hens that survive by scavenging. The performance of the local Criolla breed was tested on 12 farms, each of which was given six hens. The birds were fed 70 grams of local feed, and otherwise scavenged during the day. The results are shown in Table 12. The Criolla hens are described as phenotypically very variable, probably as a result of introgression from exotic breeds. However, they are adapted to the high altitude, cold weather and scavenging conditions.

TABLE 12
On-farm egg production of Criolla hens in Bolivia over eight months

Production parameter	Performance
Rate of lay (%)	55.8
Egg weight (grams)	52.6
Adult body weight (grams)	1 982

Source: Altamirano (2005).

Table 13 summarizes the results of performance studies of indigenous breeds conducted during the last 15 to 20 years, complementing the information presented by Horst (1988). Although, some of these breeds are described as indigenous, they may have been crossed with exotic breeds, which may have increased the number of eggs laid.

It is clear from Table 13 that management system strongly influences performance. Under a scavenging system in which hens are used for brooding, the laying rate is 10.3 percent – corresponding to 38 eggs per year. The figure increases considerably if the hens

TABLE 13
Summary of studies of egg yield and growth rate in local hens

		Field					Station			
Traits		Rate of Lay (%)			Daily gain (grams/day)		Rate of lay	Hatchability (%)	Daily gain (grams/day)	
Feeding		Fed	Scavenging		0–20 weeks	0–10 weeks			0–20 weeks	0–10 weeks
Country	**Breed**		Brood	No Brooding						
Islamic Republic of Iran		37.5					64			13.6
Thailand	TIC		9.6							
Viet Nam	Ac						27	67	6.9	
	H'Mong						33	68	10.5	
	Mia						38	73	18.9	
	Ri						43	85	11.3	
India	Kadaknath				6.2					
	Nicobars						46		8	
Morocco			15	21.3						
Kenya	Normal			11.4			23			
	S. feather						32			
Nigeria		19.2	6.2				34.0			
Tunisia							34.8			
United Republic of Tanzania			8.7		5.3					
Malawi					7.5				10.6	
					7.1					
Ethiopia			12.7	20.4						
Bangladesh	Deshi		13.2			3.5				
Egypt	Fayoumi						42.4	77		5.9
	Fayoumi GG						60.8	88		9.0
	Fayoumi PP						65.1	89		7.9
Senegal			16.4							
Bolivia				55.8						
Average		28.4	10.3	27.2	6.5	3.5	41.7	78.1	11.6	9.1
Horst (1988)			16.9				24.5			

do not have to brood. Laying rates reported in the more recent studies are higher than those reported by Horst (1988) – more so for station data than for data recorded under field conditions. Horst (1988) did not differentiate between different types of field data. However, assuming that the three types of field management are represented in the same proportions in Horst's data as in the later studies, the increase in laying rate is 5.1 percentage units. The equivalent increase for station data is 17.2 percentage units. Leaving aside the effect of improving feeding and management over the 20 years, it could be postulated that the considerable increase in the station-recorded data is the result of the introgression of exotic breeds into the "local" populations. This introgression has probably also taken place in the hens used for the field tests. However, because of the large genotype × environment (G × E) interaction, the genetic improvement is poorly manifested under field conditions (see the section on G × E interaction, below, for a fuller explanation).

3. BROODING AND NATURAL INCUBATION

Broodiness is a characteristic of native hens. When a hen becomes broody, it will stop laying and start incubating eggs and will later care for the hatched chicks. The onset of incubation is coincident with a complete regression of the ovary, a considerable regression of the comb, and a characteristic clucking. The broody hen performs persistent nesting, turning and retrieval of the eggs, and defence of the nest. When the chicks are hatched, the hen will brood and defend them, and will continue the characteristic clucking.

Broodiness is initiated physiologically by an increase in the concentration of the hormone prolactin beyond a threshold that is three to four times higher than that which is present during the egg-laying phase (Scanes, 1986). This shift is stimulated by the perception of a nest with eggs (Johnson, 1986). After having taken care of the hatched chickens for two to three months, the hen develops its reproductive organs again and is ready to start a new laying period. Thus, two to four cycles can be completed per year.

High egg yield and broodiness are antagonistic traits. Domestic hens bred for high egg production have more or less lost their ability to become broody, because many generations of selection for higher egg production have favoured genes that hinder the onset of the broody period. Artificial incubation has been used for almost 100 years, during which time no interest has been given to the ability to incubate. Romanov *et al*. (2002) studied the inheritance of brooding by crossing a White Leghorn strain that did not show any sign of brooding with a Bantam strain for which the incidence of hens becoming broody was 79 percent. The hens were observed for a period of 28 weeks during which light intensity was reduced and hard-boiled eggs were left in the nest. Careful analyses of the various cross combinations led the authors to the conclusion that a previous theory of sex-linked inheritance of broodiness had to be rejected, and that the genetic variation across the two races was caused by incomplete dominance on at least two autosomal loci (ibid.).

While broodiness is looked upon as a hindrance to high egg yield under commercial production conditions, smallholder poultry production systems in developing countries require hens that are able to incubate the eggs, because artificial incubation is not possible. The Bangladesh Model (see the section below on breeding programmes involving crossbreeding through parent stock) involved a system based on two exotic breeds in which the parent stock was kept on breeding farms spread around the country. The original idea was to incubate the hatching eggs in rice husk incubators, but during the colder periods of the year this did not work, and therefore local hens (locally termed Deshi hens) were often used to incubate.

Two recently published studies investigated the incubating capacity of Deshi hens in Bangladesh. Azharul *et al*. (2005) compared the effects of clutch size and hen weight on hatchability and chick survival. Roy *et al*. (2004) compared two types of artificial incubation to natural incubation in terms of hatching success and subsequent chick growth and survival. In both studies, hatching eggs were from the Rhode Island Red × Fayoumi cross, while the broody hens were located in two villages and kept under farm conditions.

In the study undertaken by Azharul *et al*. (2005) broody hens were divided into two groups according to their body weight and were set with a clutch size of 8, 11, 14 or 17 hatching eggs. The overall hatchability rate of fertile eggs was 87 percent; neither the size of the mother hens nor the clutch size seemed to influence the hatching results. The only significant effect observed was in chick survival after eight weeks – the chicks of small hens (800–950 grams) survived at a rate of 95.4 percent, while the chicks of large hens survived at a rate of 87.4 percent. This difference was statistically significant. Thus, small hens were better able to incubate a clutch of 17 eggs weighing 41 grams and raise a group of about 15 chickens to 8 weeks of age under village conditions in Bangladesh than were larger hens. This underlines the opinion sometimes met among some smallholder farmers that dwarf hens are better at reproduction (see section on preferences for free-range local chickens, below).

Roy *et al*. (2004) divided 960 hatching eggs into three groups: the first distributed among 24 brooding hens; the second placed in a rice husk incubator (see Box 1); and the third in a conventional electric incubator. The natural incubation proceeded as described by Azharul *et al.* (2005), while incubation in the electrical incubator followed the recommendations of the manufacturer.

The study recorded a similar hatchability (88–89 percent) for fertile eggs placed in the electrical incubator and the rice husk incubator. Eggs placed under the brooding hens had significantly higher hatchability (92 percent). The different incubation methods had no effect on growth and survival rate up to six weeks of age in confinement rearing.

BOX 1
The rice husk incubator

The principle of a rice husk incubator is as follows: Pillows containing rice husk are placed in sunlight until the temperature of the pillows reaches 39 °C. The hatching eggs are tied up in bundles of 20 eggs using red cloth, and they are also heated in the sunshine. Upon reaching the right temperature, the bundles of 20 eggs are placed in the incubation cylinder between two heated pillows. At four-hour intervals the eggs are moved from the incubator and turned. Pillows that have cooled to less than 39 °C are exchanged with newly heated pillows. It is ensured that the eggs remain at a temperature of at least 37 °C.

In Pakistan, Farooq *et al*. (2003) ran a study on hatching performance in 13 villages, with ten farmers randomly chosen from each village. It was an observation study of actual practices in the Peshawar District in the North West Frontier Province. Focus was on the hatchability rate of set eggs, duration of egg storage, season, clutch size, number of hatching cycles per hen, and breeds of hen. The overall hatchability rate was 60.8 percent. There were 14 eggs per clutch and 4.1 clutches per year. Among the breeds used, Fayoumi hens had an 8 percent poorer hatchability rate than the Deshi hens and the Rhode Island Red hens. When it is not possible to control the storage temperature, the duration of the storage period has a great influence on hatchability. This is particularly important during the summer, when it is hot. The farmers were to some extent aware of the problem, but hatchability was nevertheless poor during the summer, as can be seen from Table 14.

The hatchability of set eggs was significantly higher in spring and autumn. The authors explain this finding by pointing to the more favourable conditions for egg storage during these seasons, combined with greater availability of fresh eggs. Even though the summer eggs are stored for a shorter period, hatchability is poor, which must be a result of the high storage temperature.

The basic problem with the development of chicken embryos is that they have already developed to the gastrula stage during egg formation. At oviposition, the eggs should be cooled to below 27 °C to stop further embryonic development for at least a day. This is not always achievable during the summer in tropical areas. Another factor is the storage period. Sørensen *et al*. (2003) recommend that at temperatures between 18 °C and 26 °C, eggs should not be stored for more than three days before being set for incubation, while eggs at a storage temperature of 16 to 17 °C may be stored for up to seven days without reducing hatchability. Farooq *et al*. (2003) found, by regression, a 2.48 percent reduction in the hatchability rate for every additional day of storage. These are average figures for the whole year – the rate of reduction may be higher during the summer.

The overall conclusion from the studies cited above is that indigenous hens provide good egg incubation under low-input systems if the storage conditions are adequate, and particularly if there are enough fresh eggs. The drawback is that it is difficult to produce large numbers of chicks at the same time – for which the rice husk incubators might be ideal. It should also be borne in mind that egg production stops completely during the incubation and brooding phase. From a genetic resource point of view, indigenous hens are vital for maintaining a natural source of egg incubation, given that the high-yielding

TABLE 14
Hatchability of set eggs under natural incubation in Peshawar district, Pakistan

	Summer	Autumn	Winter	Spring
Hatchability rate	46.5^{c}	70.8^{b}	47.9^{c}	78.0^{a}
Age of eggs (days)	6.28	12.5	14.0	9.25

Means in a row with no common superscript differ significantly (P<0.05).
Source: Farooq *et al.* (2003).

breeds have been manipulated to such an extent that they are unable to survive without the support of humans.

4. GENETIC RESISTANCE TO DISEASES

Genetic resistance to diseases is considered here because it is generally assumed that there are considerable variations among breeds with respect to their ability to withstand and survive pathogenic infections. In large-scale commercial poultry production it is common to vaccinate against pathogens that may harm the birds. Smallholder farmers regularly face constraints that make vaccination difficult to implement. It is, therefore, very important that birds kept under such systems have sufficient heritable robustness to withstand the high levels of disease challenge to which they are exposed.

Hutt (1949) in his book *Genetics of the fowl* mentioned that imported stock is usually susceptible to diseases and parasites to which it has not previously been exposed. Already at that time, several reports from various part of the world had described how breeders were crossing native stock with imported stock with the objective of producing birds that combined the good features of both. Hutt noted that the native stocks' resistance to the diseases present in particular production environments had been developed by natural selection to such an extent that the genes of these birds made a contribution to the crossbreeds that was just as important as that of the imported genes. To emphasize the importance of local environment, he mentioned that a stock of red junglefowl originating from Southeast Asia was much more sensitive to the poultry diseases prevailing around Cornell in the United States of America than were American birds.

Reports on the performance of indigenous chickens in developing countries often leave the reader in doubt as to whether the birds actually have the superior disease resistance that is often claimed for indigenous breeds. Further investigation often reveals that an important proportion of mortality is caused by predators; another factor may be that in some periods of the year birds are undernourished and are consequently more susceptible to infectious diseases. Rahman *et al*. (1997) report a field study in Bangladesh in which the mortality rate excluding predation varied from 16 percent to 35 percent among different strains/breeds over a laying period of 9.5 months. Accordingly to FAO (1998) mortality rates recorded in Africa vary very widely, ranging from 1 percent reported in a work from Ethiopia to more than 80 percent recorded in the United Republic of Tanzania. Further it was found that under traditional management in Africa the mortality of chickens up to six weeks was 60 percent, with 45 percent of the surviving chickens dying between six weeks of age and sexual maturity, leaving the farmer with 22 percent of the hatched chickens surviving.

During the last decade, organic egg production has become popular in western Europe. In Denmark, 15 percent of egg production takes place according to organic production standards. In these production systems, access to free-range areas creates problems comparable to those experienced in semi-scavenging systems in developing countries. The birds used in organic egg production are genetically the same as those used for caged egg production. After a couple of years of organic egg production, disease problems emerged that had never been seen in the cage systems (Permin *et al*., 2002); national industry statistics for Denmark have shown hen mortality in organic systems to be 15–18 percent per year in spite of vaccination–compared to 5–6 percent for hens kept in cages (Anonymous, 2004). These figures excluded predation, because the farmers had no data for this, but there are indications that 5–10 percent of losses were caused by foxes, sparrow-hawks and buzzards.

Thus, the mortality rates in an organic system in western Europe are almost as high as those in smallholder poultry production in developing countries. Moreover, the organic hens kept in western European climates have much better feed conditions. These hens have been bred for egg production in cages and they are not genetically adapted to free-range conditions where they receive no prophylactic treatment. The indigenous hens are genetically adapted to their environments, but they experience conditions that are far from optimal. It would be interesting to know whether, if indigenous hens were fed adequately, their mortality rates would markedly fall, perhaps to lower than those found among commercially bred hens raised under organic conditions in Europe. There is no clear answer to this question. However, a Bangladeshi study (Rahmann *et al*., 1997) showed an insignificantly higher mortality among high-yielding Lohmann Brown hens than among Sonali hens under smallholder conditions with semi-scavenging feeding. The Sonali hens derive their good disease resistance from the Fayoumi breed.

Genetic resistance to diseases can be improved in a breed or population in two different ways:

- selecting and breeding the birds that have shown ability to survive infections; and
- using molecular methods to choose breeding animals with genes or markers for genes that are known to give a better protection against infection.

The former actually represents two methods. The simple or empirical method is to ensure that all candidates for becoming parents are exposed to pathogens. Those that survive have proven resistance, the genetic element of which will be transmitted to the next generation. This is how indigenous chickens have been selected for adaptation to locally present pathogens. A more refined approach, available to commercial breeding companies, is to make an offspring test. An offspring test involves producing a number of offspring from each breeding candidate and placing them in an infected environment. The rate of mortality due to infectious diseases in the offspring groups is a direct measure of breeding value for disease resistance in the parents, and can be used to inform the selection of birds for breeding.

The second approach – selection using marker information – is still under development, and its efficiency has not yet been convincingly demonstrated. It is still rather costly to use, and therefore the use of such methods for selection in indigenous breeds is a couple of decades ahead of us.

The mechanisms behind genetic resistance are far from being fully understood. Basically, however, genetic resistance can be either resistance to infection, which will prevent the pathogen from becoming established in the animal, or resistance to disease, which prevents or reduces the development of pathological symptoms in animals infected with the pathogen. To date, selection for resistance has been based on an empirical approach. For example, Cole (1968) made use of an offspring test to obtain lines resistant of susceptible to Marek's disease after four generations. Cole's idea was grasped by the breeding companies, but soon afterwards a vaccine to control Marek's disease was developed and genetic resistance was not needed to control the disease.

The last couple of decades have brought a number of new discoveries in the field of genetic resistance (Axford *et al*., 2000), which can be categorized into two types:

- quantitative non-specific disease resistance; and
- pathogen-specific effects – a number of genetic loci have been identified where allele-specific effects are associated with resistance to specific diseases.

The major histocompatibility complex (MHC) plays a prominent role in the second type of genetic resistance, because it displays an extraordinary level of genetic variation in most vertebrate species, with very large numbers of haplotypes; allele-specific disease resistance has been demonstrated in many species for a wide range of pathogens.

In chickens it has been well known for many years that the B21 haplotype provides good protection against the Marek's disease-inducing virus in birds from a broad range of breeds. However, it is also becoming clear that a number of other non-MHC genes play a role in protection against the disease (ibid.). This B21 haplotype is found in almost all outbred populations of chickens, including the jungle fowl. According to Axford *et al*. (2000) other MHC alleles are associated with genetic resistance to avian leucosis, fowl cholera, *Salmonella* and coccidiosis.

In population studies it is common to detect many haplotypes. Schou *et al*. (2007) were able to distinguish 24 MHC haplotypes in the indigenous Ri breed, which is widely kept in northern Viet Nam; a population study showed that one of the haplotypes exerted incomplete resistance to the helminth *Ascaridia galli*. In a subsequent study involving experimental infections, the finding was confirmed in hens from the same breed and repeated in the Chinese commercial breed Luong Phuong (Schou *et al*., 2008). Lin and Lee (1996) report different susceptibilities to a very virulent Marek's disease virus among five strains of indigenous breeds. The birds suffered high levels of mortality when exposed to infection with the virus, but mortality was lower in one of the lines – indicating a genetic resistance mechanism.

Singh *et al*. (2004) discusses work that has been ongoing for some time at the Central Avian Research Institute, Izatnagar, India. The institute has developed a two-way cross known as the CARI Nirbheek, which is intended as a substitute for native scavenging chickens, especially for the remote villages where prophylactic treatment of poultry diseases is not possible. The parents of the CARI-Nirbheek were the native Aseel breed and the high-yielding CARI Red breed. An immunocompetence test was carried out, including data for humoral response such as haemaagglutinin antibody and mercaptoethanol resistance, along with phagocytic index and cellular-mediated immune response, and some other non-specific immunoresponses. In a total score index for immunocompetence traits, the two breeds used as parent stock for the CARI Nirbheek, had a considerably better immune response than the high-yielding breeds such as White Leghorn and broiler-type birds. The CARI Nirbheek had a better immunocompetence than its two parent breeds.

Thorp and Luiting (2000) report a Dutch experiment in which chickens were divergently selected for high or low antibody response. The high-responding chickens had a lower body weight. This is in concordance with resource allocation theory (Stearns 1976) and follows the prediction by Beilharz *et al*. (1993) of unfavourable genetic correlations between production traits and disease resistance: increased investments in one class of traits will result in fewer resources allocated to the other.

In contrast, comparisons between indigenous Bangladeshi chickens and Fayoumi chickens demonstrated that the Fayoumi had just slightly better resistance to Infectious Bursal Disease (IBD) (M-E-Elahi *et al*., 2001). In a comparison of Nigerian local chickens and broiler-type exotic chickens (Okoye and Aba-Adulugba, 1998) the local chicken had a lower resistance to IBD. IBD, caused by the IBD virus, is a poultry disease that seems to have evolved in commercial poultry; it was not seen in indigenous poultry until recently. Thus, indigenous populations cannot be expected to show adaptive genetic resistance to this virus.

Genetic resistance to the two most important viral pathogens in rural poultry, those causing avian influenza and those causing Newcastle disease, has not yet been convincingly demonstrated. In the case of Newcastle disease, Gordon *et al.* (1971) report a significant but small difference in mortality after six generations of divergent selection based on offspring tests after challenge at two weeks of age. The authors found a consistently higher mortality in the susceptible line, but continued selection failed to increase the divergence between lines. Age-specific ability to respond to infection is an important parameter in non-specific resistance in chickens, as the immune system is not fully developed at hatch and the chick has to rely on maternal protection. Pitcovsky *et al*. (1987) found it possible to select for high early response, and that mortality after *E. coli* infection was reduced by a factor of three in the high-resistance line compared to the low-resistance line.

Most poultry kept in free-range scavenging systems are infected with various sorts of parasite. Helminth parasites have been quite intensively studied in recent years. Endoparasitic worms can be found in large numbers in the birds' intestines. It has been established that although they do not directly cause disease in the host, they weaken the immune system and can therefore cause increased susceptibility to other more harmful disease agents. A study by Permin and Ranvig (2001) showed that high-yielding Lohmann Brown hybrids had lower worm burdens and worm-egg excretion than the traditional breed Danish Landrace following infection with the helminth *Ascaridia galli*, which indicates that some sort of genetic resistance exists. A study of the Vietnamese Ri breed and the Chinese commercial breed Luong Phuong demonstrated that a particular MHC-haplotype was associated with a statistically significantly lower infection rate with *A. galli* (Schou *et al*., 2007; Schou *et al*., 2008) (see above for further details of these studies).

To summarize:

- A considerable number of genes are known to exert resistance to disease, but they seldom provide complete protection.
- Much remains unknown about genetic resistance to diseases. In recent years, focus has been on identifying genes with specific resistance. This work has shown that in many cases resistance involves numerous genes with minor effects and that there may be interactive effects among genes (Thorp and Luiting, 2000).
- High-yielding birds that are kept in large commercial enterprises under very hygienic conditions and are vaccinated against all pathogens present in the locality will have low mortality rates. If such stock is moved to a smallholder environment without vaccination, it will suffer high mortality.
- Stocks raised for many generations in a given area can be expected to show adaptive genetic resistance to the infections prevailing in the area. However, this may not protect them sufficiently if they are moved to other environments, because the effect

of resistance genes often is often associated with a particular set of environmental factors.
- If a local breed is replaced by exotic stock, considerably better hygienic conditions and a comprehensive programme of vaccination will be required.

5. MAJOR GENES THAT CAN BE IDENTIFIED BASED ON THE PHENOTYPE

There are a number of genes with major effects on the phenotype that seem to be of special interest for poultry keeping in smallholder systems in developing countries. They can be split into three categories:

- feather-reducing genes;
- genes that reduce body size; and
- genes controlling plumage colour.

Chickens have no sweat glands. Thus, if they are exposed to high ambient temperatures, they have to rely on panting or heat loss from the surface of the skin to control their body temperature. Normally feathered chickens have a well-covered body, which protects them from losing body heat. Many local flocks include several birds with naked necks or frizzle feathers – characteristics that allow better heat dissipation from the skin. The naked-neck condition – featherless skin on the neck, on the breast, and on ventral part of the thigh – is caused by an incomplete dominant gene termed Na (Mérat, 1986). Na/Na chickens have no feathers on 30 to 40 percent of the body surface; heterozygote Na/na chickens have no feather cover on 20 to 30 percent of the body surface. According to Crawford (1976) the genotypes can be visually distinguished, as the heterozygotes have a tuft of several dozen feathers on the front of the neck.

Frizzling is caused by a single incomplete dominant gene, known as F. In homozygotes, the shafts of all feathers are extremely recurved and the barbs are curled. In the heterozygote, only the contour feathers are recurved. These birds are not able to fly, and the feathers are easily broken off by crowding. The homozygotes, in particular, may look bare. There are modifying genes that make the extent of curling less extreme (Hutt, 1949).

A number of investigations of the production ability of birds with these genotypes under both temperate and hot conditions have been carried out. Mérat (1990), summarizing a great number of studies of climatic effects on body weight at 8–10 weeks, concluded that at temperatures above 25–26 °C chickens having the Na naked-neck gene grow at a faster rate than normal (na/na) chickens, and that above 30 °C feed efficiency is better than in the normal birds.

Mathur and Horst (1990) compared the Na gene and the F gene for frizzling in two controlled settings – at normal (22 °C) and high (32 °C) temperatures – as well as in an open-house system in Malaysia with temperature variation (22 °C to 32 °C), and concluded that both the Na gene and the F gene resulted in better growth and higher egg yield at high temperatures. Combining the F and the Na genes gave a higher yield, but the effect was less than purely additive.

Haque *et al*. (1999) compared the meat yield of native Bangladeshi naked-neck Deshi (NaD) chickens to that of their crosses with Rhode Island Red (RIR), White Leghorn and Fayoumi. For growth up to 17 weeks, the NaD × RIR had the highest daily gain among the crosses. However, no clear conclusions were drawn, except that the crosses involving

TABLE 15
Performance of naked-neck crosses on smallholder farms in Bangladesh

	Na × RIR	Na × Fayoumi	Sonali (RIR × Fayoumi)	Fayoumi
Weight at sexual maturity	1142[bc]	1034[c]	1326[a]	1197[b]
Rate of lay (%)	16.7[bc]	12.0[c]	32.0[a]	22.4[b]
Age at sexual maturity (days)	201[b]	195[b]	222[a]	201[b]

Means in a row with no common superscript differ significantly (P<0.05).
Source: Zaman *et al*. (1984).

Fayoumi had a much lower mortality rates than the other crosses – 3.3 percent as opposed to 14–33 percent.

Another study from Bangladesh (Zaman *et al*., 2004) compared the cross-bred offspring of Na cocks and RIR and Fayoumi hens to pure-bred Fayoumi birds in terms of egg production capacity to the age of 46 weeks. Hens were distributed to 54 farms, each of which was given five hens at 18 weeks of age. Results are shown in Table 15. It can be seen that the rate of lay of the Sonali (RIR × Fayoumi) hens is about twice that of the Na crosses. However, the Na crosses start to lay at an earlier age.

Dwarfism

Dwarfism is caused by a single gene and is known in many species to reduce total body mass by 20 to 40 percent. In chickens, there are several loci associated with dwarfism. For example, the sex-linked recessive gene dw was used to produce the French broiler Vedette, in which the broiler mother was dwarf. The dwarf form found in most indigenous populations seems to be inherited autosomally. However, it is uncertain whether it involves a recessive gene as suggested by Somes (1990). The relatively high frequency of dwarfism seen in many countries suggests the involvement of a dominant gene. The reasons for keeping dwarf hens in regions where meat production is the major objective of poultry keeping may seem peculiar, but Njenga (2005) learned from farmers in Costal Kenya that dwarf hens had better reproductive capacity, and in particular better mothering ability; this was confirmed during work in Bangladesh by Azharul *et al*. (2005).

Njenga (2005) reports a study in Kenya in which 149 hens of different phenotypes (normal, naked neck, frizzle and dwarf) were randomly selected from rural flocks equally distributed across four ecozones in coastal areas. The hens (maximum age 12 months) were then placed in pens at a research station; they were weighed and egg production was recorded. Results are shown in Table 16.

The adult naked-neck phenotypes have a significantly larger body weight than the other phenotypes, but this is not reflected in a significantly higher early growth rate. It may be that the better growth under high temperatures thought to be associated with the naked-neck phenotype occurs at a later stage, during which the chickens sustain a higher metabolic rate per unit of body surface. The dwarf phenotypes are smaller, as would be expected, but it should be noted that they have higher laying capacity than the other phenotypes in the study.

TABLE 16
On-station production performance of naked-neck, frizzle and dwarf phenotypes and their normal counterparts in Kenya

	Phenotype			
	Normal	Naked Neck	Frizzle	Dwarf
Mature weight of mothers (kg)	1.3^{b}	1.4^{a}	1.3^{ab}	1.2^{b}
Rate of lay in 176 days (%)	23	33	27	36
Egg weight (grams)	42.5	45.8	43.0	38.1
Daily gain to 5 weeks (grams/day)	4.4^{a}	4.5^{a}	4.2^{ab}	3.6^{b}

Means in a row with no common superscript differ significantly ($P<0.05$).
Source: Njenga (2005).

Yeasmin and Howlider (1998) studied a sample of normal and dwarf local hens (Deshi) collected from a district in Bangladesh at the age of 32 weeks and kept in confinement for the next 36 weeks with free access to feed. The shank length of the dwarf birds was 30 percent shorter than that of the normal birds, and their body size was 5 percent smaller. Over the 36 weeks, the rate of lay was 33.5 percent for the dwarf and 24.7 percent for the normal birds – a difference that was found to be significant. Apart from the eggs of the dwarf hens being lighter, no significant differences were found between the two phenotypes for a large numbers of egg characteristics.

Rashid *et al*. (2005) studied the effect of dwarfism on reproduction, meat yield and feed efficiency in the cross-bred offspring of Bangladeshi dwarf hens from the indigenous population and RIR, White Leghorn and Fayoumi cocks. As the majority of the chosen dwarf hens were heterozygotes, the offspring were segregated into dwarf and normal body-sized chicks. All normal-sized chicks were discarded at the age of six weeks. The reproduction and growth of the cross-bred chicks was recorded under station conditions; the chicks were fed ad lib. At 20 weeks of age, the body weights of the dwarf RIR, White Leghorn and Fayoumi cross-bred chicks were, respectively, 7, 14 and 8 percent lower than their normal-sized counterparts. These reductions are less than that found in the Deshi hens from which the gene originated. For the White Leghorn crosses, the dwarf gene reduced bone length by 16 to 20 percent. Body weight was much less reduced – giving the dwarf chicks a much more compact form. It is concluded that the dwarf gene has an intermediary or even dominant effect rather than being recessive, as dwarf phenotypes occur in the first generation crosses, while the dwarf allele is not known to segregate in the three exotic breeds.

To conclude, the major genes causing reduced feathering and reduced body size may improve growth capacity, but perhaps not until a late phase of growth. It also appears that the naked-neck gene has a greater effect than the frizzling gene. The dwarf gene (or genes) reduces body size including some reduction in the length of the long bones. The fact that dwarf genes occur in farming systems in which meat production is the main objective could be explained by the fact that they have better reproductive capacity than the normal-sized hens and are therefore favoured by natural selection and/or in farmers’ choice of birds for reproductive purposes.

The genes that control feather colour interact to a great extent. They can be grouped into three categories: plumage-colour genes; plumage-pattern genes; and feather-pattern genes. Many of the characteristic colours found in chickens require special combinations of genes from two or three loci. The only simple example is the gene that gives rise to the white feathers of the White Leghorn breed. This gene, usually termed I, inhibits the development of colour based on eumelanin. It is incompletely dominant. Uniform black colour, as found in Black Australorps, requires the so-called E gene – the most dominant gene in the multi-allelic series affecting plumage pattern – but also requires the recessive ii gene (Smyth, 1990).

The plumage colour of indigenous chickens shows great diversity, varying from white to black with all kinds of intermediate plumage patterns. The main reasons for this great variation are the preferences of the local farmers as well as the effects of the many cockerel exchange programmes implemented for development purposes. In general, producers prefer to have dark-coloured hens, because they are subject to less predation. Njenga (2005) concluded that farmers in coastal Kenya favour red/brown birds, followed by, black and then white. The farmers like red birds because of their role in traditional medicine. Black chickens are liked because of their use in rituals involving children and because they are better camouflaged against predators. White chickens are used for traditional sacrifices.

6. CHARACTERIZATION OF GENOTYPES BY MOLECULAR METHODS

It is claimed that many local breeds in developing countries are uniquely adapted to a particular production environment. Several studies of the production characteristics of such breeds have been undertaken (see the section on local breeds, above). However, these tests have often been carried out on stations, which means that adaptation to the birds' normal production environment has not been tested. Adequate assessment of adaptation would require testing all potential breeds under the conditions specific to the respective production environments; comprehensive studies of this type have not been done.

Evidence for a genetic background for local adaptation in indigenous breeds is summarized below. In theory, local adaptations should be traceable on the basis of genotypic differences between breeds. Over the last 10 to 15 years, a number of studies have been undertaken based on the technique of tracing the segregation of microsatellites, blood groups and plasma proteins. These investigations aim to determine the genetic distances between breeds, enabling the evaluation of local breeds as genetic resources. Microsatellites are DNA sequences with a core motif of 1 to 6 base pairs repeated several times. It has been found that many breeds/populations can be distinguished on the basis of variations in microsatellite loci. The loci tend to be polyallelic, with up to 51 alleles found in one study (Qu *et al*., 2004) which covered 78 breeds. Microsatellite DNA does not code for any known proteins, but it is found across the genome and is often closely linked to coding genes.

Msoffe (2003) investigated the genetic diversity of nine local ecotypes in the United Republic of Tanzania, on the basis of 16 microsatellites with 4 to 15 alleles per locus across all breeds. A White Leghorn strain was used as a reference. The genetic variability within the local ecotypes, measured in terms of the number of alleles per locus and by heterozygocity, was slightly higher than that found in a similar study in South Africa (van

Marle-Köster and Nel, 2000). The author argued that this could be explained by genetic introgression from exotic cockerels. Using spatial genetic analysis (Nei *et al*., 1983), much of the genetic difference between ecotypes was shown to be associated with geographical distance. By using individual dendograms to cluster the 130 chickens analysed, it was shown that for three ecotypes all chickens were located in the same cluster, while other ecotypes were more mixed. This indicates that some of the ecotypes had been subject to genetic introgression over time. The work of van Marle-Köster and Nel (2000) was based on five strains kept under rural conditions in South Africa, one strain from Mozambique and one from Botswana. The study revealed high levels of genetic variation, with 23 microsatellites out of 27 being polymorphic, with an average of 6.1 alleles per marker. The heterozygosity varied from 31 percent in an isolated population known as Koekoek to 60 percent for two free-ranging lines from Botswana and Mozambique.

Qu *et al*. (2004) reported a comprehensive study from China that included 78 strains/breeds from all over the country with 30 to 50 birds per breed. By using 27 microsatellites they found 18.6 alleles per locus across all breeds and a heterozygosity varying from 55 percent to 65 percent. Calculating the genetic distances between all the breeds and constructing a phylogenetic tree, they demonstrated that the 78 breeds could be divided into eight subgroups, which generally corresponded to geographical locations. This sample of strains or breeds is probably the largest investigated so far. At two of the loci, the authors described 51 alleles, which is almost twice as many as in the European project AVIANDIV1 in which 52 populations were studied (Rosenberg et al., 2001; Hillel *et al.*, 2003). This high level of genetic variation relative to European poultry indicates that the Chinese breeds may indeed constitute an important genetic resource, both in terms of local adaptation and selection potential.

Ya-Bo *et al*. (2006) studied 12 indigenous breeds from southern China, of which ten had been included in the study by Qu *et al* (2004). Thirty microsatellites were used of which 11 were identical to loci in the earlier study. Sixty birds per breed were sampled. Ya-Bo *et al*. (2006) calculated correlations for polymorphism information content (PIC) and heterozygosity estimates across the two studies, and found correlation coefficients of 0.67 and 0.38 respectively. Heterozygosity is a locus-specific quantity, which is expected to differ depending on the identity and number of markers included in a given study. Therefore, the lower across-study correlation for heterozygocity can be explained by the use of different microsatellites. The PIC measure is a more relevant parameter for comparing different investigations. Both the Chinese investigations depicted genetic distances between breeds by constructing phylogenetic trees. The European study undertaken by Hillel *et al*. (2003) calculated pairwise genetic distances between each of the 52 breeds included in the study; it is argued that this method is better than the construction of phylogenetic trees as a means to identify rare breeds that are of value for future conservation and breeding efforts.

In Jordan, Al-Atiat (2006) studied indigenous birds from four areas, which had a wide range of morphological differences, some were from ancient breeds from Pakistan and Egypt, and some were commercial hybrids. Calculation of genetic distance by the Nei (1972) method revealed a distance of 0.14 between the indigenous and the ancient breeds and 0.21 between the indigenous and the commercial hybrids. The largest distance (0.29) was between the commercial and the ancient breeds. In India, Parmar *et al.* (2004) used three varieties of the indigenous Kadaknath breed to evaluate the genetic variability within this breed by means of 25 microsatellites, all polymorphic in all three varieties. A phylogenetic consensus tree was constructed, which grouped all three varieties into one cluster; the genetic distances using the Nei method varied from 0.0951 to 0.1943, which led the author to conclude that there was negligible genetic distance between the three varieties.

Microsatellites provide a tool that enables populations to be distinguished by means of a statistical measure of genetic distance. This is a valuable tool for identifying populations that are priorities for conservation. The data currently available indicate that rural poultry breeds represent considerable genetic variation and that divergence can be detected among breeds – indicating a basis for local adaptation. However, it has to be noted that microsatellites are merely markers on the DNA, and are not directly associated with genes that express the product we actually are interested in. As adaptation involves non-neutral loci, theory would suggest that these diverge more quickly than neutral markers in locally adapted breeds. Indeed, several studies have demonstrated faster differentiation in quantitative genetic markers than in neutral molecular markers (a comprehensive summary can be found in Leinonen et al., 2008).

The recent complete mapping of the chicken genome (International Chicken Genome Sequencing Consortium, 2004; International Chicken Polymorphism Map Consortium, 2004) will provide tools with which to address such questions much more precisely. A review by van Tienderen *et al*. (2002) discusses how the detection of local adaptation can be improved by development of functional genetic variation assays targeting single nucleotide polymorphisms (SNPs) or sequence-specific amplification polymorphisms (SSAPs). When we have sufficient knowledge of variation in specific relevant genes, we can study local breeds to detect unique alleles that affect nutritional requirements, disease resistance, brooding behaviour and other traits that are necessary for the survival of the species under rural conditions.

7. CONSUMER'S PREFERENCE FOR FREE-RANGE LOCAL CHICKENS

Poultry meat

It is evident that in both commercial markets and rural indigenous poultry meat markets local chickens are sold at a higher price than broilers. In India, Khan (2004) observed that indigenous birds were sold at a price of US$1.5–2.1 per kg compared to US$0.7–0.9 per kg for commercial broilers. In the United Republic of Tanzania, Mlozi *et al.* (2003) found that local chicken meat was priced higher than meat from broilers, and also higher than beef, fish and beans; thus, the indigenous chickens were priced higher than any of the comparable protein sources. The reason could have been the multiple uses of the indigenous chickens for cultural and ritual purposes as well as food, but may also relate to the fact that the indigenous chickens taste better than broilers for many consumers. Bell (1992) reports that local chickens are preferred because of their pigmentation, leanness, taste and suitability for use in the preparation of special dishes. Gnakari *et al.* (2007) compared the organoleptic quality of local chickens in Côte d'Ivoire to that of their crosses with broilers. The comparison was carried out using eight-week old chickens fed a broiler diet containing 20 percent protein, and raised at a temperature of 35 °C, but which were otherwise

TABLE 17
Organoleptic test of chicken meat quality in Côte d'Ivoire

	Local chicks	Hubbard	F1-crosses
Weight at 8 weeks (grams)	860^{c}	2 233^{a}	1 190^{b}
Feed conversion ratio	2.8^{2}	1.54	2.39
Tenderness	6.7^{a}	1.9^{b}	6.1^{a}
Taste	6.3^{a}	3.7^{b}	5.4^{a}
Smell	6.8^{a}	2.8^{b}	5.6^{a}

Means in a row with no common superscript differ significantly ($P<0.05$).
Source: Gnakari *et al*. (2007).

raised using the techniques common in the area. The organoleptic test was carried out by a panel of 15 persons who were trained to score the tenderness, taste and smell of the roasted meat on a scale of zero to ten. Seventy chickens per breed were tested. The results are presented in Table 17.

The test panel preferred the local chickens; surprisingly the F1 crosses were much closer to the local chickens for all the parameters examined.

Eggs

Eggs from local hens are considerably smaller than eggs from commercial layers – usually weighing 50 to 66 percent less. In spite of the difference in size, the market price for local egg is often higher than for eggs from commercial hens. The eggs of local hens may have specific qualities (e.g. the Fayoumi breed is known to lay small eggs with a large yolk), but the laying capacity of these breeds is rather poor. Tixier-Boichard *et al*. (2006) worked with this idea and crossed Fayoumi cocks with ISABrown layers and compared laying parameters and yolk sizes for the Fayoumi, the ISABrown and their crosses from the start of laying to the age of 63 weeks; the birds were kept in individual cages and fed a commercial layer mash. The main results are shown in Table 18.

The example shows that Fayoumi have genes that are of interest if the objective is to produce eggs with a high proportion of yolk, or just to produce yolk mass. There may be other low-producing breeds whose eggs have special qualities of interest for the future from the commercial point of view.

Breed utilization depends to a great extent on farmers' preferences. The choices may be based on the money that the farmer can obtain by selling chickens or chicken products, but may also depend on the colour of the plumage or on the temper and behaviour of the birds. Barua and Yoshimura (1997) report that among smallholders in Bangladesh, coloured indigenous fowl are more acceptable than international hybrids, because of their motherly instincts (i.e. broodiness), and because they can be used to incubate and rear chicks under rural conditions; their camouflaged plumage, alertness and fighting character enable them to protect themselves and their chicks from predatory animals. The study conducted by Njenga in coastal Kenya (Njenga, 2005) showed that normal birds were preferred to naked

TABLE 18
Yolk size and yolk proportion of Fayoumi and ISABrown chickens and their crosses

Breed	Age at first egg (days).	Laying rate, per hen housed 20–62 weeks.	Egg weight at 40 weeks (grams)	Yolk weight (grams)	Yolk mass (kg)	Yolk/ albumen ratio (%)
Fayoumi	136[c]	55.4[a]	42.8[a]	15.0[a]	2.44[a]	63.2[c]
ISABrown	127[b]	89.0[b]	58.8[c]	15.7[b]	4.11[b]	42.3[a]
Fayoumi × ISA Brown	125[a]	84.2[b]	51.6[b]	16.3[c]	4.04[b]	54.4[b]

*Means in a column with no common superscript differ significantly (P<0.05).
Tixier-Boichard *et al*. (2006).

neck, frizzle or dwarf birds, although the naked neck was known to grow faster. Only the normal birds could be presented to visitors as a gift; the frizzle birds could be used only for rituals and for home consumption. The dwarf was ranked fourth because of its small size; however, it has a good reputation for mothering ability (cf. the study by Azharul *et al.* (2005) of Deshi hens in Bangladesh).

Thus, the local hens seem to have qualities other than production capacity that affect both consumer acceptance of the product and farmer preferences (management and cultural factors). Some of the local breeds may be of interest for commercial production, because they have genes for special production traits that could be of interest in the future (see the above discussions of yolk size in the Fayoumi, shell thickness in the Fulani breed of Nigeria, and the growth curve of the Mia breed of Viet Nam).

8. OPTIONS FOR GENETIC IMPROVEMENT UNDER SMALLHOLDER CONDITIONS

The smallholder farmer can intervene in several ways to influence which birds become the parents of the next generation. Such actions range from buying a cock to mate with the existing hens to record-based selection of the hens or buying high-yielding cross-bred chicks for meat or egg production. The most common approach has been to implement cock-improvement programmes.

Comparisons and crosses of indigenous with exotic chickens

There have been a number of studies of the performance of crosses between local and exotic breeds. The major objective of such crosses has been to combine the environmental adaptations of the local chickens with the better production capacity of the exotic chickens. Box 2 provides a brief discussion of crossing effects.

The works cited in the following paragraphs include some studies of pure exotic breeds and of crosses between different exotic breeds.

In the Islamic Republic of Iran, Ansari *et al.* (1997) compared the native Isfahani breed (NF) with the crosses AA♂ × NF♀, AA being chickens in which the Arbor Acre broiler type was the male grandparent stock. Daily gain during the first 16 weeks was recorded to be 10.6–11.2 grams for the pure NF and 17.1–17.4 grams for the crosses under station conditions with ad libitum feed.

BOX 2
Crossing effects

It is important to note that the heterosis (or hybrid vigour) effect is often quite high for traits and characteristics that influence reproduction and fitness. Heterosis is based on genetic dominance effects. It can be expressed as the percentage superiority of the crosses over the average of the parent breeds. It is not unusual to have 25 to 40 percent heterosis in the first generation of crossing (the F1 generation). It is important to bear in mind that further breeding of the crosses to produce F2, F3 (etc.) generations will, in theory, make the heterosis effect disappear. Heterosis is expected to be reduced by half in the F2 generation, and the reduction is often even higher. As such, the heterosis effect will more or less disappear after a couple of generations. Continuous crossing to an exotic cock will transform the original local population, making it identical to the breed from which the exotic cock derives. After six generations only 1.56 percent of the genes from the local birds will be left, and there will be almost no heterosis effect. To maintain the full heterosis it is necessary to maintain pure-bred parent stock and to continue to make F1 crosses. Further discussion of heterosis can be found, for example, in Falconer and Mackay (1996).

At Pantnagar in India, Sharma (2004) compared local chickens from villages surrounding a research centre to the offspring of local cocks mated with White Leghorn (WL), Rhode Island Red (RIR) and Black Australorps (BA). The test was performed under station conditions and the birds reared on deep litter with free access to feed. Some results are shown in Table 19.

The laying capacity of the local hens is particularly poor compared to the crosses. However, the question remains as to whether this picture would hold if the test had been carried out under realistic farm conditions. The heterosis was around 8 percent for egg production traits, and almost non-existent for daily gain – which is consistent with the usual findings of crossing experiments.

Another study done in India (Singh *et al.*, 2004) deals in greater depth with the particular requirements of breeds that face the challenges of predators, disease, periods of low food availability, high temperatures and the need to be able to brood. The CARI Nirbheek chicken was developed to produce under such conditions (ibid.); it is a two way cross which has an annual laying capacity of 163 eggs and a survival rate of 90–95 percent under field conditions if supplemented with 30 grams of feed per hen per day. Under comparable conditions, the traditional scavenging chickens achieved an annual lay of 45 to 60 eggs with a survival rate of 70–80 percent. The two parent breeds of the CARI Nirbheek are the native Aseel breed and the CARI Red. The Aseel is known for its high majestic gait and its dogged fighting qualities, which provide good protection against predators. It also has a reputation for being well adapted to tropical conditions and has been found to be the most immunocompetent in tests comparing it to a number of other breeds (Singh *et al.*, 2004). The CARI Red breed, which was used as the mother, has been selected for improved

TABLE 19
On-station performance of crosses of local hens with exotic breeds at Pantnagar in India

	Local hens (L)	Local × WL	Local × RIR	Local × BA
Daily gain to 20 weeks (grams)	5.1[a]	6.1[b]	6.3[b]	6.1[b]
Age at first egg (weeks)	29.0[a]	23.9[c]	24.5[bc]	26.0[b]
Rate of lay to 72 weeks of age (%)	30.0[a]	61.7[d]	56.9[c]	53.4[b]

Means in a row with no common superscript differ significantly (P<0.05).
Source: Sharma (2004).

performance under tropical conditions and has been recorded as having an annual egg production of 180 eggs, with an egg weight of 65 grams.

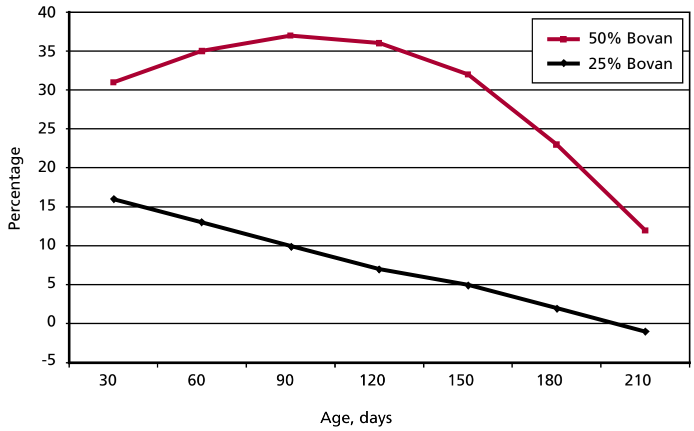
Sørensen and Ssewannyana (2003) describe a programme in which cocks from the brown-egg layer hybrid Bovan Brown were crossed with local hens under field conditions in Uganda. In a study involving ten farms, chickens with 0, 25 or 50 present Bovan Brown genes were raised to six months of age. The 25 percent Bovan cross was obtained by back crossing the F1 hens to local cocks. The daily gain of the 50 percent Bovan cross proved to be superior to that of the local chicks by 30 percent at one month of age, increasing to 38 percent at three months of age, after which the superiority decreased gradually (ibid.) (see Figure 1). The 25 percent Bovan had a 15 percent superior daily gain at one month of age, after which the advantage was gradually lost, with no difference in gain remaining at 6 months of age. No report on reproductive capacity and general fitness of the hens with Bovan genes was obtained in the Uganda study, but observational data indicate a higher mortality rate in the hybrid hens as the project continued. The conclusion is that crossing with the exotic breed introduces a faster early growth that more or less disappears by the traditional market age. Thus, if such a cross is to provide benefits, it is important to ensure that the chickens can be marketed at an earlier age.

Omeje and Nwosu (1986) report that in Nigeria the hybrid known as Golden Link was crossed with indigenous hens, and the F1 generation was backcrossed to the Golden Link or to the local breed. The chickens were housed in confinement at a station to the age of 20 weeks. Daily gain of the backcross to the local hen was 8.8 grams per day; daily gain was 27 percent higher in the backcross to the improved hybrid; a backcross to the F2 resulted in an intermediate value for daily gain. No difference in egg production was observed between the two groups.

Hens from three ecological zones in Nigeria were collected and crossed with the exotic breeds Dahlem Red (DR) and Dahlem Red Dwarf (DRD) (Adedokun and Sonaiya, 2002). The chickens were raised and kept at a station with free access to feed. Some performance characteristics are shown in Table 20.

In Malawi, the Black Australorp breed has been the preferred exotic breed for many years for crossing with indigenous breeds; Kadigi *et al*. (1998 and 2001) describe the production capacity of such crosses. Both studies involved a diallelic crossing; in the first, the authors evaluated the performance of cocks at 20 weeks of age, and in the second they studied egg production traits. Both studies took place at stations with free access to feed. The results are shown in Table 21.

FIGURE 1
Comparison of body weight of local and cross-bred chicks under field conditions in Uganda



Note: Percentage superiority to local chicks at various ages with respect to body weight.
Source: Sørensen and Ssewannyana (2003).

The results indicate that crossing with the exotic breed considerably improved egg production, but growth capacity was little changed. The proportion of breast meat in the carcass was 15–16 percent (the figure for modern broiler chickens slaughtered at the same body weight is 25 percent).

Also in Malawi, Phiri (2003) compared Black Australorps with a cross between Black Australorps and Hyline under three management systems: free access to feed, semi-scavenging and scavenging between the ages of eight and twenty weeks. Until eight weeks of age, the chicks (all males) remained at the station with free access to feed. After the eighth week, one third of the birds were left at the station while the rest were moved to a village and distributed to farmers, who were each given 16 birds. Half of the participating farmers were provided with supplementary feed, 35 grams of which were provided to each bird

TABLE 20
On-station performance of Dahlem Red crosses with Nigerian native hens

	DR	Native	DR × Native	Dwarf*
Daily gain to 20 weeks (mixed sex) (grams)	10.9[a]	7.7[c]	9.4[ab]	6.2[d]
Age at 1st egg (weeks)	22.9	22.7	22.4	23.1
Number of eggs laid in 280 days	150[a]	100[c]	120[b]	87[c]
Rate of lay (%)	57.8[a]	38.3[c]	45.6[b]	33.7[c]
Egg weight (grams)	55.7[a]	36.8[c]	42.9[b]	42.0[b]

*Native Dwarf♂ × DRD♀.
Means in a row with no common superscript differ significantly ($P<0.05$).
Source: Adedokun and Sonaiya (2002).

TABLE 21
On-station performance of Black Australorp (BA) crosses with Native chickens in Malawi

	Year	BA × BA	NC × NC	BA♂ × NC♀	NC♂ × BA♀
Daily gain of males to 20 weeks (grams)	1998	16.3[a]	12.7[c]	15.3[b]	14.9[b]
Breast meat (% of carcass)	1998	15.4[a]	15.5[a]	15.2[a]	16.3[a]
Dressing percentage	1998	70.5[a]	71.6[a]	70.6[a]	70.3[a]
Daily gain to 8 weeks (grams)	2001	6.1[a]	5.3[b]	6.1[a]	5.4[b]
Age at 1st egg (weeks)	2001	22.0[b]	22.6[a]	22.9[a]	21.9[b]
Rate of lay to 28 weeks (%)	2001	33[a]	17[c]	24[a]	20[b]

Diallel crossing of Black Australorps (BA) and native chicks (NC). Birds had free access to feed.
Means in a row with no common superscript differ significantly (P<0.05).
Sources: Kadigi *et al.* (1998); Kadigi *et al.* (2001).

every day (SS) The other farmers were not given any supplementary feed (FS). The results from these experiments are shown in Table 22.

The birds kept on station with free access to feed had the highest bodyweights; but as feed was costly, the returns were higher the less feed was used. The full scavenging system therefore yielded the highest returns. There was a tendency (not statistically significant) for the cross to show better growth under the harsh environment with scavenging feeding, while the pure Black Australorps grew better at the station.

Altamirano (2005) compared the local breed Criolla in the highland part of Bolivia with the commercially marketed hybrid Harco. Harco is a cross of Rhode Island Red♂ × Barred Plymouth Rocks♀ and has been demonstrated to be an excellent layer under free-range condition when supplemented with 50 grams of feed per day (Vries, 1993). Six hens each were distributed to 24 farmers in several villages located at an altitude of 3 200 to 4 500 metres above sea level. The hens were fed 70 grams per day of, respectively, a commercial diet with 11.9 MJ of metabolizable energy (ME) per kg and 18.7 percent crude protein (CP), a local diet with 12.3 MJ ME/kg and 13.8 percent CP, and pure maize with 14.4 MJ ME/kg and 9.3 percent CP. The results of the experiment are shown in Table 23.

Harco had significantly better production level under all three feeding regimes, but because of the higher cost of the Harco hen, the local hen supplied with local feed is almost as good as the Harco in terms of net profit. The poor performance of Criolla fed on commercial diet was a result of the birds not being used to the fine-ground feed.

Comparisons of local breeds with exotic breeds almost always show an advantage for exotics when the tests are carried out at stations. Investigations carried out under actual field condition remain scarce. In addition, most of the exotic breeds tested are not high-yielding hybrids of the type used in the international poultry industry.

The semi-scavenging poultry production model developed for smallholders in Bangladesh used the cross combination RIR♂ × Fayoumi♀ – a hybrid which is known as the Sonali. The Fayoumi is a breed developed in Egypt to yield at a modest level, but which is particularly renowned for its genetic resistance to disease. The RIR is basically an American

TABLE 22
Comparative performance and economic returns of Black Australorp and its crosses with Hyline under station and field conditions in Malawi

	Station ad lib		Field SS		Field FS	
	BA	BA × HY	BA	BA × HY	BA	BA × HY
Daily gain, 7–20 weeks (grams).	18.3[a]	17.3[a]	14.1[b]	15.6[b]	11.2[c]	11.5[c]
Weight at 20 weeks (grams)	2299[a]	2189[ab]	1860[c]	2032[bc]	1437[d]	1563[d]
Carcass as % of body weight	66.3[a]	64.8[a]b	62.9[b]	63.9b	62.5[bc]	60.8[c]
Gizzard, liver and neck as % of carcass	7.4		8.6		9.3	
Returns (income-cost)* (US$/chick)	-0.12	-0.26	0.17	0.27	0.34	0.42

Means in a row with no common superscript differ significantly (P<0.05).
BA = Black Australorp; HY = Hyline; SS = supplementary feeding; FS = no supplementary feeding.
*Cost of: 6 week chickens = US$0.92; feed = US$0.30 per kg; carcass = US$1.93 per kg; medication = US$0.14/chick.
Source: Phiri (2003).

TABLE 23
Comparative performance and economic returns of local hens and the hybrid Harco under field conditions in Bolivia

Breed	Harco			Criolla		
Feed	Commercial	Local	Maize	Commercial	Local	Maize
Rate of lay in 8 month (%)	76.6	73.3	56.6	46.6	56.6	40.0
Egg weight (grams)	61.1	57.9	52.9	52.3	52.6	51.9
Mortality (%)		7.6			6.3	
Body weight (kg)	2.07	2.05	1.90	2.02	1.97	1.82
Costs (US$/placed hen)	3.25	3.25	3.25	1.80	1.80	1.80
Feed cost (US$/hen)	3.01	2.53	1.88	3.01	2.53	1.88
Sale of eggs (US$/hen) (US$0.5/egg)	6.90	6.60	5.10	4.20	5.10	3.60
Return (US$/hen)	0.64	0.82	-0.03	-0.61	0.77	-0.08

Source: Vries (1993).

breed that is nowadays used as one of the parent breeds of the brown-shelled high-yielding hybrids used by most commercial producers. The RIR used in Bangladesh have not undergone this last step of selection to a small hen purely for laying.

In order to make a more thorough investigation of the possibility of using the commercially available hybrids, an investigation was carried out in Bangladesh under field conditions, in which each smallholder farmer was given 4 to 6 female chickens from one of eight different breed combinations at eight weeks of age. The study involved about 300 farmers in three districts in Bangladesh (Rahman *et al*., 1997). The hens were kept according to the general management practices in those areas, which meant that the birds were allowed to

TABLE 24
Performance, mortality and economic returns of breed combinations based on Lohmann Brown, Fayoumi, Rhode Island Red and White Leghorn

	Lohmann Brown	(A×R) × Fa	Fa × AB	R × AB	Sonali (R×Fa)	R × WL	(R×Fa) × AB	WL × AB
Age at 1st egg (weeks)	35	32	32	34	33	32	33	35
Egg/hen day actual	86^{b}	104^{ab}	86^{b}	105^{ab}	119a	97^{b}	86^{b}	99^{ab}
Egg/hen day 365 d	140^{ab}	137^{b}	125^{b}	139^{ab}	156^{a}	128^{b}	141^{ab}	139^{ab}
Mortality %	22.1^{ab}	35.0^{b}	27.6^{ab}	32.6^{b}	15.9^{a}	25.2^{ab}	21.2^{ab}	22.8^{ab}
Supplement feed, kcal	146^{a}	122^{b}	136^{ab}	144^{b}	130^{a}	134^{ab}	146^{b}	135^{b}
Gross Margin,$	3.08^{b}	3.88^{ab}	2.58^{c}	3.03^{b}	4.68^{a}	3.31^{b}	3.01^{b}	3.54^{b}

Means in a row with no common superscript differ significantly (P<0.05).
AB = Lohmann Brown; Fa = Fayoumi; R = Rhode Island Red; WL = White Leghorn; A = Male line of Lohmann Brown.
Daily feed intake for a hen is around 300 kcal.
Gross margin = value of eggs and spent hen – value of 8 week pullet and supplementary feed during the growing and laying period.
Source: Rahman *et al*. (1997).

scavenge during the day and were supplemented with household waste, farm by-products or small amounts of grain. The hens were not used for brooding, and prophylactic treatments to protect against infectious diseases were given. Egg production, mortality and supplementary feed use were intensively recorded until the hens were 1.5 years old and had been laying for about nine to ten months. Results are presented in Table 24.

It can be observed that the Sonali is better than any other breed. This superiority is not significant for the individual traits, but in the overall gross margin the Sonali is significantly better than all combinations except one. Of particular interest is that the production of the commercial Lohmann Brown in terms of egg laying is less than half that they achieved in caged environments in the European Random Sample test (Sørensen, 1997a); this underlines the importance and power of genotype × environment interactions.

The lesson from these various experiments is that the majority of crosses have an improving effect on growth and egg yield even in field tests under smallholder conditions, but information on health and reproductive capacity is scarce and the information available is not promising (Taddelle *et al*., 2000). The Bangladeshi Model and the Indian work with the CARI Nirbheek, in which the smallholders have to recruit new cross-bred birds, seem promising. However, the costs involved were so high that the approach did not work in Bangladesh (see the section on breeding programmes). Results of crossing experiments based on the introduction of exotic breeds have to be interpreted carefully because heterosis is a temporary effect that disappears after a couple of generations.

Genotype × environment interaction

Given the low production capacity of local hens, why should we not simply promote the use of high-yielding hybrids and thereby obtain much more eggs and meat? The example illustrated in Figure 2 demonstrates the complexity of the matter, and that the relative productivities of local and exotic breeds are sensitive to genotype × environment interactions.

The traditional attitude in animal breeding has been that "the character required is best selected under environmental conditions which favour its fullest expression" (Hammond, 1947), and this trajectory has been followed to a great extent by breeders up to the present day. The statement means that the candidates from among which the parents of the next generation are to be chosen should be kept in an environment that (in the case of laying hens) maximizes the egg production of the individual hen. Among the more important environmental factors to be optimized are:

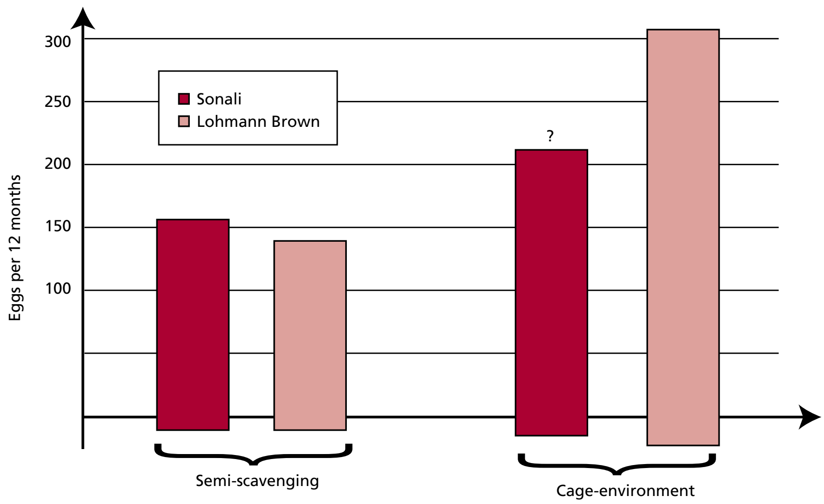
- absence of infectious diseases;
- minimum stress; and
- a sufficient and balanced diet.

It is generally considered that the elite birds of the breeding companies are kept under very hygienic conditions. It is also clear that these hens have been kept in individual cages for many generations, which implies that their laying pattern has not been disturbed by a social interaction to establish ranking order. In terms of genetic capacity, this strategy of management has produced hens with a high egg yield when conditions are optimal. This means that the hens should be kept in a well-equipped cage system, have free access to a balanced diet, and have a high standard of hygiene involving a prophylactic programme including vaccination. If these conditions are not met, we may expect an increased risk of poor production, because the ancestors of the hens:

- have not been exposed to infection pressure for many generations and have therefore have not undergone indirect selection for disease resistance;

FIGURE 2

Breed × environment interaction for egg production in semi-scavenging conditions in Bangladesh and a cage environment in Germany



The value for the Sonali in the cage environment is a guessed value.

- have not been disturbed by interplay with other hens while being recorded for laying capacity and therefore have not undergone direct selection for the ability to handle social interactions with the other hens in a flock;
- have not been exposed to predators and therefore have not undergone direct selection for the ability to protect themselves and their chicks;
- have had free access to a balanced diet and therefore have not undergone direct selection for the ability to cope with suboptimal diets or low food availability; and
- been selected for eggs laid in the cage and therefore have not undergone direct selection for the ability to perform normal nesting behaviour in connection with egg laying.

So far, we know that:

- native and local breeds and Red Jungle Fowl seem to have better genetic resistance to infection, and they are often better able to defend themselves and escape from predators;
- the willingness of the "cage-adapted" breeds to lay their eggs in nests has decreased, which means that farmers with free-range hens have considerably more work in collecting the eggs; an experiment demonstrated that the floor laying rate of such "cage-adapted" breeds was reduced to the half over five generations of selection for laying rate based on a trap-nest system in a floor system (Sørensen, 1992; Sørensen, 1997b); and
- high-yielding hens often show high levels of cannibalism and feather pecking in free-ranging production systems where they are kept under floor conditions with free access to each other (Sørensen, 2001).

Going through the literature on the subject of genotype × environment interactions, the main conclusion emerges that the probability of a genotype × environment interaction increases with the difference between the environments or the genetic distance between the breeds. Figure 2 gives an excellent example. We know that the Lohmann Brown was able to produce 303 eggs in 12 months under optimal conditions in a German Random Sample test (Sørensen, 1997a), while during the same time it produced 140 eggs under semi-scavenging conditions where the Sonali hens produced 156 eggs. The production capacity of Sonali in the German Random Sample has not been tested, but a result far below 300 eggs and slightly above 200 eggs might be expected. Thus, we are faced with a typical G × E interaction.

N'Dri *et al.* (2007) studied a slow-growing breed used in France for "Label rouge" production which has to take place under free-range conditions. Selection for a better feed conversion ratio (FCR) requires measurement of the individual feed intake of chickens in individual cages. The study showed that it was more efficient to improve FCR in a free-range system by indirect selection for a change in the growth curve by postponing the age at the inflection point, than selecting directly for FCR in cages (ibid.). The indirect measures could be done on chickens reared under free-range conditions. This demonstrates the importance of taking G × E interactions into account in selection schemes.

The mechanism behind the G × E interaction is described in Box 3.

BOX 3
Example of genotype × environment interaction

Consider a breed selected for high egg yield in cages with free access to balanced feed (Env. A). Imagine that over five years there is an improvement of ten eggs/year above the background rate of 300 eggs/year, meaning that the breed obtains a production capacity of 310 eggs/year. Imagine also that the unselected parent stock was tested in a suboptimal environment in which it produced 150 eggs (Env. B). Our expectations for yield in Env. B after the improvement would be 155 eggs, assuming that the genetic coefficient of variation remains identical, i.e. that the same genes are of importance for egg production in the two environments. In this case, we can consider the five extra eggs in Env. B to be the correlated response to the increase obtained by selection in Env. A – a genetic correlation of one between egg production in Env. A and in Env. B.

When this genetic correlation across environments (cross-environment correlation) is less than one, we speak of a genotype by environment (G x E) interaction. G × E interactions occur in the example above if the genetic improvement obtained in Env. A results in an increase of less than five eggs when the birds are tested in Env. B. This can be attributed to the fact that different genes affect egg laying in the two environments. There are complicated statistical–mathematical methods for performing these types of calculations, but a simple approximation can be done by looking at the overall means. In the above example, imagine that the improved breed produced 152 eggs in Env. B instead of the expected 155 eggs. These two-fifths, or 40 percent, can be regarded as the proportion of genetic variation that is common for egg production in the two environments, while the remaining 60 percent of the genetic variation that influences egg production in Env. A does not influence egg production in Env. B. According to the concept of set theory, 40 percent of elements are common to both, which is close to saying that the correlation is 0.4. This concept was first introduced by Robertson (1959) and later explained by Falconer and Mackay (1996).

It is also possible for the cross-environment correlation to be less than zero, causing different genotypes to perform best in different environments. Figure 2, showing egg production in Sonali and Lohmann Brown layers in Germany and Bangladesh, respectively, offers an example of this phenomenon. This requires that genes with a positive effect on egg production in Env. A have directly negative effects in Env. B. Cross-environment correlations of less than zero have been shown in model organisms, for example for egg size in butterflies (Steigenga *et al.*, 2005). When the genetic correlation is less than one, selection in an inappropriate environment (Env. A) can result in animals that perform poorly in comparison to the unselected stock in Env. B.

Taking account of G × E interaction in selection for rural local chickens

When trying to improve local breeds through a selection programme it is very important to be aware of the consequences of G × E interactions. Among the environmental influences mentioned by Horst (1985), three should be considered: housing, feeding and temperature.

There is no doubt that cage systems differ so much from free range systems that there will be a G × E interaction when birds developed through an egg selection programme based on single cage system are kept in free-range condition (see Sørensen, 1997b). Therefore, the objective should be to find a means of selecting for higher egg yield under conditions that are close to the rural conditions under which the birds will have to produce.

Considerable G × E interaction was observed when broiler-type chickens were selected for higher early growth rate on a 22 percent protein ration and the resulting birds tested on a 17 percent protein ration, and vice versa; the genetic correlation for growth capacity under the two feeding treatments was 0.4 (Sørensen, 1986). A review by Sørensen (1985), reports considerable indications of genetic variation in adaptability to reduced concentrations of important nutrients such as amino acids. Thus, breeding birds under selection for increased performance should receive a ration similar to that which they can be expected to receive in the rural areas, in particular if some nutrients may become limited.

It is well established that birds from small breeds adapt better than larger birds to high ambient temperature (Horst, 1985). Detailed genetic studies of small and large breeds in a temperate climate (Berlin) and a hot climate (Kuala Lumpur) showed that the genetic correlation of egg yield measured in the two environments was low (0.34 to 0.17), while body weight had a somewhat higher genetic correlation (0.73 to 0.78). The consequence of these genetic correlations is that for egg production, 10 percent genetic progress achieved in Berlin would be manifested by a 1.7 to 3.4 percent increase in Kuala Lumpur, while for body weight a 10 percent genetic improvement achieved in Berlin would be manifested by a 7 to 8 percent increase in Kuala Lumpur (Horst 1985).

Breeding programmes

Before starting a breeding programme the following issues have to be addressed:

- The breeding goal has to be defined. In many cases, the main issues relate to the question of whether the output should be meat or eggs, or perhaps a combination. Other traits may also be important to include in the breeding goal, but it is very important that they are measurable. Such other traits or characteristics include plumage colour or form, and other anatomical specialties that might be of importance for religious or other rituals.
- Cross-breeding has proved to be a success in the commercial systems that use high-yielding hybrids. The question is whether a cross-breeding model suitable for smallholder farms in developing countries can be developed.
- A decision has to be taken as to what to do with the existing local populations if they become part of a crossing programme or are replaced by the introduction of commercial hybrids or other exotic breeds.

Genetic improvement of chickens for smallholder systems where birds are kept under free-range conditions should aim to produce birds that have increased performance under conditions where balanced feed, hygienic standards and good management are limiting factors. It can be debated whether the best approach is to begin with high-producing breeds and adapt them to the environment or to begin with low-producing but well adapted local breeds and try to improve their production levels. From a theoretical standpoint, it can be argued that complex traits such as disease resistance tend to have a lower heritability than morphological traits such as growth, and therefore we might expect that progress could more easily be obtained by selecting local breeds for higher production than by adapting high-yielding breeds to cope with disease pressure and feed limitation. Conversely, the advantage of the high-yielding breeds with regard to production traits might be greater than the advantage of the local breeds with regard to survival traits. Methods aiming to introgress exotic genes into local populations could potentially exploit the advantages of both, but unless such measures are carefully planned and well executed they may result in a disruption of the local adaptations of the indigenous breeds. In addition to such production-related considerations, the social importance that local birds have for the smallholder farmers for gift giving and religious rituals has to accounted for; this may mean that in some cases the improvement of local breeds is the only way forward.

In most cases, the actual choice has been to utilize high-yielding breeds from abroad either to cross with the local birds or to replace them. The lack of clear success is often a consequence of the critical dependence of the programmes on improvements to the birds' environment. This does not always happen, and if it does the effect may be temporary. Even when it does happen, seasonal effects or disasters may completely negate the improvements, resulting in the farmers being left once again with the original non-improved local breed. In India there are attempts to improve local breeds with the CARI Nirbheek bird (Singh *et al*., 2004). Hazary *et al*. (2004) demonstrated that at limiting levels of nutrition (poorly balanced diet) there was still a considerable heritability for traits such as growth and egg production, indicating that improvement under smallholder conditions would be possible.

Thus, to improve genetic capacity under smallholder conditions there are basically three ways to implement a breeding programme:

- cross-breeding through recurrent replacement of birds;
- introgression of exotic cocks; and
- genetic improvement of local breeds.

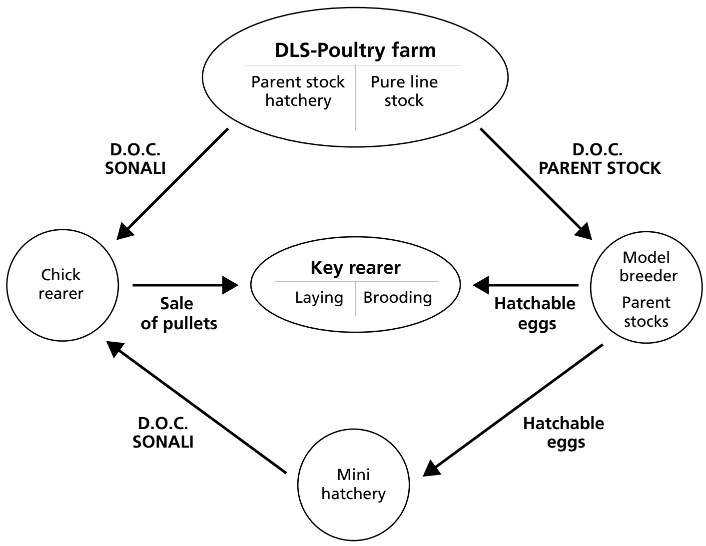
Cross-breeding through parent stock

The model used in Bangladesh for a number of years, often referred to as the Bangladesh model, (see Figure 3) was based on a complete utilization of cross-breeding effects.

The two breeds Fayoumi and RIR were maintained by the Directorate of Livestock Services (DLS) in Bangladesh with the purpose of supplying birds to the villages. This supply was achieved either by crossing the two breeds on the DLS farms to produce F1 chickens which were then transferred to local chick rearers, or by transferring Fayoumi female and RIR male birds to model breeders (see Figure 3). The cross-bred chicken from this model is known as the Sonali; it has had a good reputation among the Bangladeshi smallholders. In several comparisons including the study by Rahman *et al*. (1997), it proved to be the highest-yielding breed combination for hens kept under semi-scavenging conditions.

The period in which this model was introduced was characterized by the involvement of many enthusiastic people and strong financial support through donations. It later became clear that such a complex structure was too ambitious for a developing country where crucial inputs such as quality feeds and timely medication could not be relied upon. Furthermore, the flow of birds through the multiplication and cross-breeding phases often

FIGURE 3
The Bangladesh model



The middle group of operators were all located in the villages where there are one model breeder, one to two chick rearers and many key rearers that produce eggs. The model operated with a mini hatchery (see section on brooding and natural incubation) for each serving groups of two to four villages.
D.O.C. = day old chicks.
Simplified after the original (DANIDA, 1997).

broke down, as new parent stock was not readily available. The farmers' acceptance of the Sonali hen also changed over time as they discovered that they could not reproduce its good performance, which as an F1 cross involved considerable heterosis. Subsequently, new development programmes decided to use pure-bred Fayoumi hens, with which the smallholders can breed continuously without the need to buy new chicks every generation. Obviously, running cross-breeding programmes requires the participation of staff with a good understanding of the mechanisms involved at all levels of the project, all the way from breeding and keeping the parental lines to organizing multiplication through the parent stock.

More recently, Indian researchers have proposed models based on a cross-breeding programme with the CARI Nirbheek chicken (Singh *et al*., 2004). In this project there seems to be a good understanding of the necessity to develop the cross-breed so that it is able to cope with the semi-scavenging conditions under which smallholders keep chickens in the relevant area of India. This Indian model deviates from the Bangladesh model in that one of the parent breeds is a local breed (the Aseel) that is genetic adapted to the environment. However, the model requires that F1 chickens are continuously produced and that the smallholders are persuaded to buy these chickens once a year. There is as yet no published evidence regarding the success, or otherwise, of utilizing such a cross-bred chicken for laying purposes.

The ultimate solution could be to introduce high-yielding hybrids from the commercial breeding companies to the smallholder sector, taking advantage of the experience gained in running a cross-breeding programme and establishing functional multiplying programmes, but from various sources it has been reported that such chickens have a poor performance under smallholder conditions (Rahman *et al*., 1997; Singh *et al*., 2004; Tadelle *et al*., 2000). The problem is that the very high production capacity of these cross-bred birds results in very high metabolic demands, and they perform badly unless they are provided with sufficient and balanced feed, hygienic conditions and protection from predators.

In conclusion, a functional model for cross-breeding through parent stock requires a stable production and management system with a high cost, which makes it hard to reconcile with the actual reality facing smallholders in developing countries. Governmental organizations or commercial breeding companies need to be willing to develop breeds and cross-breeding programmes that take account of the local conditions, and to sustain the supply of birds, feed and medication – as was done in the initial phases in Bangladesh and with the CARI Nirbheek in India. The experience of the Bangladesh model shows the difficulties involved in implementing such a programme in a low-input system even if cross-bred hens with considerably better production capacity are available. The cost of the annual recruitment of new hens was too high and the multiplication programme could not be relied upon.

Cross-breeding through cockerel exchange/introgression

Another way of utilizing cross-breeding is a cockerel exchange programme of the type practised for many years in developing countries. The simplest method is to supply the smallholders with improved-breed cocks. When the genes of the new cock contribute to the next generation, the birds will often grow faster and become larger; they will often also differ in plumage colour. If the village or region is exposed to an unfavourable season when there is a shortage of feed or subject to an outbreak of infectious disease, these cross-bred chickens with outstanding genes for growth will often be the most vulnerable and will die. That is why several reports have concluded that such programmes have no lasting impact apart from increasing the variation in plumage colour.

Tadelle *et al*. (2000) report that in Ethiopia the extension service of the Ministry of Agriculture promoted schemes in which cockerels from selected strains were reared to 15–20 weeks of age and then exchanged for local cockerels owned by smallholder farmers in order to raise the genetic status of the local poultry population. The impact of this strategy has not been sufficiently assessed; but according to the authors, the implementation of these policies has had only limited success because the high mortality rate of the exotic breeds caused by lack of adaptation to the rural environment, poor management, and susceptibility to the prevailing diseases. It is also considered that neglecting to involve the farmers in the planning stage may have contributed to a lack of success. It is further argued that such programmes need to be backed up by parallel improvements in feeding, housing and health care (ibid.).

Sørensen and Ssewannyana (2003) describe continuous back crosses to high-yielding commercial laying stock in Uganda. The Bovan Brown birds used in the project were raised at the Serere Animal and Agricultural Institute (SAARI), a governmental research station.

Before the start of the project, a meeting with the interested farmers was held in the parish involved to sensitize the farmers and to select those who had reasonable housing facilities, showed interest in buying supplemental feeds, and whose hens were less likely to be affected by the intervention of a neighbouring cock. At the onset of the project, the pure-bred Bovan cocks were given to the farmers on condition that all fertile cocks on the farm were caught and taken away. After a year, the cock was exchanged for another cock; the plan was to establish a new synthetic population at the SAARI station that had the right proportion of local and Bovan genes and then to make some genetic improvements at the station. The "right" proportion of local and exotic genes had to be established based on information on growth, egg production, survivability and success in incubating and brooding. A farmers' union was created in order to encourage the farmers to participate (e.g. in the decisions regarding the breeding goal). It was also realized that it was necessary to conserve the local breeds in case the crossing project did not proceed as planned. A project was undertaken to establish the number of distinct local populations within Uganda. Six populations have been described phenotypically (Ssewannyana *et al*., 2003); genotypic characterization remains to be finally evaluated to decide on the number of populations to be conserved.[2]

The general conclusion with regard to introgression of hybrid layer genes into local breeds is that the genetic input from faster-growing and earlier-maturing hybrids such as brown-egg layers will speed up the growth of local chickens. In order to take advantage of the faster early growth, the birds should be marketed one or two months earlier, thus saving on reduced feed costs. From the two examples described above, it is unclear what happens to the reproductive capacity and fitness of the cross-bred breeding hens when kept on the smallholder farms. Also it is unclear to which extent it is necessary to maintain a continuous supply of birds to the farmers to maintain the desired proportion of exotic genes. Finally, it is unclear to which extent it is necessary to keep a strain of pure-bred local hens in order to be ready for future utilization in the programme. Therefore, before initiating such programmes, experiments should be designed to establish the optimal level of crossing with respect to growth and reproductive capacity.

Genetic improvement of local breeds

A four-page note entitled "Some poultry breeding problems in Egypt", written in 1958 by Professor Morley A. Jull on leave from Maryland University as a poultry specialist and consultant for the United States Overseas Mission, gave some information on the situation of the Fayoumi and of attitudes to the breed at the time. He noted three local breeds in Egypt of which the Fayoumi was the most popular, it was reported to lay 156 eggs per year – 70 percent of the performance of White Leghorns at that time, but considerably higher than the 60 eggs achieved by the birds he had observed in Iraq. The Egyptian government had developed better and more profitable poultry production and they had established the Fayoum Poultry Research Station to maintain and improve the Fayoumi breed (Hossary and

[2] These observations are based on the author's experience as a consultant at the Livestock Systems Research Programme donated by the Danish DANIDA organization in co-work between the National Agricultural Research Organisation (NARO) in Uganda and the Danish Institute of Agricultural Sciences during 2000–2005

Galal, 1994). Professor Jull recommended using progeny tests to make improvements in egg production and to take mortality rates into consideration in order to obtain information on resistance to disease on a family basis. There is no information on what actually happened, but in 1994 Hossary and Galal reported progress from 134 eggs to 216 eggs per 12 months – an improvement of about two eggs per year, which is about the same as observed in the high-yielding White Leghorn breed (Flock and Heil, 2002). Over the years there have been several reports that support the view that the Fayoumi has very good disease resistance to a range of poultry diseases (excluding IBD – see section on genetic resistance to diseases, above). Thus, it can be concluded that:

- during its first century the Fayoumi breed was selected under subtropical conditions, exposed to the infectious diseases prevailing in smallholder production systems based to some degree on scavenging feeding; and
- during the last half century, the breed has been kept in a station environment, but probably fully fed and using progeny testing as a selection method that allowed progress in laying intensity similar to that obtained for the White Leghorn type of bird.

Crysostome (personal communication) had the idea of a project in West African countries to improve local breeds by gathering a sufficient sample of birds of local breeds at a central station and testing offspring as the basis for choosing parent birds for the next generation (progeny test). What sets this project apart is that the testing is intended to take place on smallholder farms where performance data are recorded and used for selection of elite birds. The key point is that selection for better egg production is based on tests performed in the environment in which the birds will have to produce (see Box 3). Some of the selected elite birds are then placed as cockerels on the smallholder farms to spread the improved genes into the local populations. This is the same principle as has been used with success in dairy cattle breeding in Europe and perhaps also in the development of the Fayoumi breed. Commercial poultry breeding companies apply more advanced methods known as reciprocal recurrent selection; such approaches are not applicable in the case of pure-bred birds. It is estimated that the programme will improve the production level of the local breeds at a rate of 2–3 percent per year, with simultaneous selection for adaptation to the rural environment. Most importantly, the improvements will be maintained in the event of breakdowns caused by climatic stress or natural disaster for example.

9. CONSERVATION AND BIODIVERSITY

The general trend in commercial poultry breeding is towards uniformity (Fimland, 2007). Production of four-way hybrids for the world market is dominated by a few companies. Although the companies offer several hybrids, many of them deviate from each other merely by the exchange of one or two of the strains. Many of the strains used by the breeding companies are rather similar – as shown by the microsatellite-based study in the European AVIANDIV1 project (Hillel *et al.,* 2003). This study included the Old Scandinavian reference population, which is actually a cross of seven international White Leghorn hybrids available on the market in 1969 and which has been kept ever since as a control population using at least 100 females and 50 males as parents in each generation. The heterozygosity level of the reference population ranked 33 among the 52 breeds included in the study, and was thus less heterogeneous than many landraces and traditional breeds. There is no reason to believe that the heterozygocity in the total population of White Leghorn strains in the commercial companies has increased since the time the reference population was established.

The fact that 20 percent of recorded livestock breeds are classified as "at risk" according to FAO's classification (with a further 36 percent being of unknown risk status), and the ongoing loss of breeds (62 extinctions reported between December 1999 and January 2006) (FAO, 2007a) have given rise to some alarm regarding the status of animal genetic resources.

In poultry, more than any other livestock species, commercial breeding has rather narrow breeding goals – either high egg production or high meat production in a high-input system – driven by economic priorities. This commercial way of thinking leaves little concern for genetic diversity. Moreover, the birds are not able to reproduce if electrical incubators are not used.

In contrast, the following management systems are likely to maintain higher levels of genetic variation:

- organic agriculture, which often requires dual or multipurpose breeds;
- low-input or backyard poultry keeping farming as practised by smallholders in developing countries, which requires genes that enable survival under suboptimal conditions; and
- poultry kept for cultural or social purposes, as ornamental breeds or for entertainment.

These approaches to poultry management are much less driven by economics.

In areas where commercial poultry production and these other management systems coexist, there will often be a conflict associated with the risk that free-range chickens may be a source of infectious diseases. Such a conflict will often result in some degree of restriction on keeping free-range poultry, forcing many small-scale producers to give up poultry keeping and sometimes placing breeds at risk.

Once the need for conservation measures has been recognized, the following steps should be taken:

- investigate the level of genetic diversity within the species and the occurrence of rare genes of importance for the species as a whole;
- evaluate the possible narrowing of genetic diversity and the risk of losing rare genes or complexes of genes;
- calculate genetic distances among the populations within a species, and establish whether there are some populations that are genetically distant from the major group and have traits or characteristics that are desirable for the species, and should therefore be conserved;
- evaluate whether some populations are in danger of being lost and should be classified as at risk; and
- establish conservation programmes to address the priorities identified.

The major questions for a conservation strategy will be: which breeds/populations should be conserved; how to conserve them; and finally who is going to pay?

The first question can to some extent be solved on the basis of measurement of genetic distances, but there will always be further issues to take into account such as the objective of conserving particular traditional breeds or particular characters/phenotypes. The *Global*

Plan of Action for Animal Genetic Resources (FAO, 2007b) notes that insufficient information hinders proper decision-making with respect to conservation programmes and calls for improved characterization and monitoring of breed populations and of risk factors.

Cryoconservation of semen has been undertaken in most poultry species; rates of success are variable (Blesbois, 2007). In establishing the French Avian Cryobank (Blesbois *et al*., 2007) a considerable variation (7 percent to 68 percent) was observed among endangered chicken lines in terms of successful production of fertile eggs using cryoconserved semen; they also found considerable variation among individual males in this respect. The way ahead seems to be a test of the fresh semen of the individual males as a predictor of semen freezability (Blesbois *et al*., 2008). Successful cryoconservation of the zygotic embryo at an early stage has not been reported, and it is difficult to imagine conditions under which it would be a reliable conservation method. Therefore, today, the safest conservation method will be continuous breeding involving sufficient numbers of birds to avoid inbreeding and genetic drift. Where such a solution is not possible, cryoconservation could be used, bearing in mind that some lines and breeds have very poor fertility after the semen has been frozen and thawed. These arguments apply to chickens and to geese. Reliable conservation could not be achieved yet in turkeys, ducks or guinea fowl (Blesbois, 2007).

In general it is the task of society to pay the costs associated with conservation – in most cases this will mean governments or other funding institutions.

10. THE WAY FORWARD

It has been demonstrated in many countries and for many breeds of poultry that smallholder production represents a unique reservoir of genetic resources. Local breeds have been shown to possess both superior levels of genetic variation relative to commercial breeds and unique phenotypic traits signifying valuable local adaptations. Considering also how smallholder poultry production affects the livelihoods of the majority of the rural population in most developing countries, and its role as a nutritional resource which cannot easily be substituted by other kinds of animal production, we recommend that future strategies focus on sustainable development of this resource. The potential eradication of local breeds through culling and restructuring for control of HPAI would be a disaster, not only for the smallholder farmer, but also for worldwide biodiversity. Further, it would be a loss for the poultry industry as some of these local breeds carry genes that may be of importance for the future development of commercial poultry breeds.

Faster progress in egg laying may be obtained by introgression of foreign genes or use of cross-breeding programmes, but such methods often require management improvements that smallholder farmers may not be prepared to adopt for economic, social or cultural reasons. Assuming the low input/output smallholder system will continue to exist in many parts of the developing world, we believe that sustainable progress in productivity of 2–4 percent per year will be possible using local chickens. At the same time, this approach would account for the need for hens that can incubate and brood, and for the cultural needs of the farmers.

Such improvement programmes would require regional breeding stations stocked with local breeds, from which genetically improved birds (mainly cocks) could be distributed to villages. Genetic improvements should be based on progeny testing on smallholder farms.

Such central facilities are often already in place – only minor reconstruction would be needed. The breeding programme should be carried out by people educated in quantitative genetics, animal breeding theory, statistics and electronic data processing. The lack of younger students with sufficient training and education in the disciplines necessary to take responsibility for a breeding programmes in poultry might be a bottleneck. Most of the academic staffs at universities and research institutes in developing countries have a veterinary background, and their knowledge and interests in genetics will tend to be focused on molecular genetics, which is of limited relevance in these circumstances. Relevant education programmes should be initiated at one or more universities that have the required capacity.

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