National rabbit project population of Ghana: a genetic case study

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Summary

The National Rabbit Project (NRP) of Ghana, West Africa, is an internationally recognised programme. For several decades, the NRP has served as a model role to the lesser developed countries (LDC) as a means to alleviate national meat shortages by providing appropriate breeding stock, training, extension support, *etc.*, to limited-resource farmers. The rabbit population at the NRP is highly heterogeneous, based on the original introduction of some sixteen exotic breeds which have been inter-crossed with local stock since 1972. In general, exotic breeds represented genes for improving production traits while the local population possessed genes for adaptation. Early cross-bred generations of rabbits reproduced and developed well at the NRP station in local conditions of climate, outdoor housing, forage-based diet, simple management, *etc.*, as opposed to exotics which generally fared poorly. Cross-breeds (F_1 animals) were reported to be "thrifty and fast growing." Distribution of cross-bred stock to farmers in villages was and continues to be successful. By 1975, the population size was 4 000 breeding rabbits. The NRP did not employ a station geneticist, so breeding goals and the selection programme were not clearly defined. However, production trait performance of the NRP stock has been at least comparable to that of other rabbit populations maintained in the LDC in adverse environmental conditions. In 1989, a formal USAID project was established between the NRP and Alabama Agricultural & Mechanical University (AAMU) entitled "Development of a Synthetic Tropical Rabbit Breed". This closed, nucleus population was genetically characterised throughout this project activity. Individual 90-day body weight data were collected from 687 rabbits representing 61 sire and 194 dam families in two consecutive generations. Paternal half-sib estimates of heritability for first and second generations were 0.41 ± 0.19 and 0.43 ± 0.18. In the past ten years, the NRP has continued to provide genetically appropriate stock to farmers; however, utilisation as a practical and sustainable means of genetic conservation largely takes place in villages.

History of rabbit rearing in Ghana and the national rabbit project

The domestic rabbit was introduced into Ghana by missionaries well over a century and a half ago. Congregations under their parishes were encouraged to raise rabbits on a backyard basis since rabbit meat was the only known meat which had no known taboos as to its consumption either on religious or ethnic grounds (Opoku and Lukefahr, 1990). In addition, rabbits were easy to handle by women and children, feeding and management practices were simple and locally sustainable, and a plentiful (albeit inexpensive) meat source was secured. Rabbit rearing on small farms has spread throughout the country.

In recent decades, Ghana's demand for agricultural food products has been greatly dependent on importations which have contributed to its foreign exchange debt. In early 1972, the Government of Ghana (GOG) was approached by Mr Newlove Mamattah (the then Liquidator of the Centre for Civic Education), who had been a backyard rabbit breeder for thirty-seven years. The GOG had the goal of establishing a viable, diversified and growing agricultural sector as a basis for economic and social development and food self-sufficiency (Technoserve, 1975). Furthermore, the GOG was keenly aware that many low-income families could not afford to include animal food products in their diet because of national meat shortages. The small-scale, self-reliant model of rabbit production ("Rabbits for Food for the Millions"), as proposed by Mr Mamattah, convinced the GOG to invest 160 000 cedis (at the time equivalent to US$184 000) as a Government equity contribution to create the National Rabbit Project (NRP). Mr. Mamattah was appointed as the NRP's first director. The NRP was established at Kwabenya on 32 ha of land, some 15 km north of Accra, with the following original aims and objectives (Technoserve, 1975; Opoku and Lukefahr, 1990):

- to encourage and enable Ghanaians to take up backyard rabbit breeding as a means of providing adequate meat for their family table at costs lower than those prevailing on the market and to encourage the development of private commercial rabbitries;
- to provide improved foundation stock for sale to backyard breeders by a scientific programme of cross-breeding and up-grading of local rabbits;
- to carry out research in order to develop a rabbit husbandry system specifically appropriate to conditions in Ghana;
- to provide field extension services which would assist backyard breeders in acquiring the technical knowledge necessary for carrying out viable breeding programmes and applying improved husbandry practices; and
- to serve as the nucleus for the development of a Ghana Rabbit Breeders association which will serve as a guide for information and services between the NRP and individual breeders.

The NRP is wholly owned by the GOG with the original intention of making a modest return on its investment. By 1977 the first national census figure of 13 948 rabbits from registered breeders was reported (Anonymous, 1979). By the end of 1979 the NRP had released over seven thousand rabbits for both breeding and consumption, including meat supplied to departmental houses, restaurants and hotels (Opoku and Lukefahr, 1990). The GOG's strong interest and financial support of the NRP and the dynamic leadership of Mr Mamattah, largely accounted for the early success of this unique programme. Mr Mamattah was also most active in publicising the NRP by participating in international rabbit conferences and workshops, providing radio interviews and publishing reports in scientific journals achieved through collaborative ventures (Mamattah, 1978; Owen, 1981). In 1976 the first World Rabbit Congress was held in Dijon, France, where the World Rabbit Science Association appointed Mamattah as Secretary for Developing Countries. Mr Mamattah's legacy stemmed from his tireless promotion of small-scale rabbit production for the LDC as a means of hunger and poverty alleviation. By the late 1970s, Mr Mamattah had retired and a new director was appointed (Mr Eugene Opoku).

NRP population background

In 1972 eighty local rabbits were used as foundation stock for the NRP. Foundation animals were purchased from backyard breeders throughout the country. Between 1972 and 1984, several hundred rabbits of various breeds: Alaskan, Blue Vienna, Californian, Champagne D'Argent, Chinchilla, Checkered Giant, Creme D'Argent, Danish Giant, Danish White, Dutch, Flemish Giant, French Lop, New Zealand White and Thuringer, were generously donated or provided to the NRP, GOG, by the Governments of Denmark, Switzerland and the United States (Lukefahr *et al.*, 1992). It was Mamattah who requested the importation of exotic breeds. The aim was to procure "good quality, beefy-giant types for crossing and up-grading the local animals" (Technoserve, 1975), despite the fact that these standard breeds were developed in temperate environments and were predominantly from and selected in commercial and (or) fancy herds. However, by 1975 the initial population of 80 rabbits had increased to nearly 4 000 rabbits.

Unfortunately, the imported breeds were reported by Opoku and Lukefahr (1990) to acclimatise rather poorly (e.g. low fertility and depressed growth) to the stressful tropical environment in Ghana, in agreement with previous studies (Damodar and Jatkar, 1985; Matheron and Dolet, 1986; Sundaram and Bhattacharyya, 1991) involving comparable breeds and environments. For example, in 1980, the Danish shipment involving 1 349 does and bucks resulted in only 54 litters born by exotic does in the following two years. Nonetheless, rabbits continued to be propagated, largely through exotic male x local female matings, cumulating in several F_1 lines to produce cross-bred stock for both farmer distribution and for the NRP as replacement stock (Table 1). Gradually, F_1 lines were pooled, mainly through *en masse* random matings among individuals in the population. In local conditions of climate, fresh forage feeding with limited supplementation and simple management at the NRP (similar to small farmer conditions), straight-bred exotics were eventually lost due to poor adaptation and (or) low reproduction and survival success (N. Mamattah, personal communication). In contrast, while F_1 and the subsequent composite populations were observed to be generally thrifty, rapidly growing and fertile, no experimental comparisons were made between composite and local rabbits to determine the extent of genetic improvement. Nonetheless, when cross-bred stock were distributed to farmers in villages (purchases by private treaty), breeding and growth performance were quite satisfactory (Lukefahr, 1998).

Table 1. Exotic and cross-bred mature stock inventory in 1975 at the National Rabbit Project in Ghana.*

Exotic breed	Surviving exotics		Born in Ghana Exotic		Born in Ghana Cross-bred	
	bucks	does	bucks	does	bucks	does
Alaska	7	0	0	1	9	9
Blue Vienna	20	4	6	12	22	24
Californian	3	1	0	0	0	0
Champagne d'Argent	6	2	0	2	1	1
Chinchilla	3	1	0	0	0	0
Checkered Giant	2	1	0	0	0	0
Creme d'Argent	9	1	6	7	0	1
Flemish Giant	3	1	1	0	10	18
French Lop	2	1	0	0	2	1
Thuringer	15	4	1	11	3	3
Total	70	16	14	33	47	57

*A total of 120 animals from Switzerland was shipped between 1973 and 1974.
Source: Technoserve (1975).

From 1984 to 1989 the period following initial exotic stock introductions, the breeding objectives and programme were not entirely clear for the heterogeneous, composite NRP population. However, based on interviews, there is evidence that replacements were selected if they had impressive 90-day, market weights (E. Opoku, personal communication). Also, closely-related matings (e.g. full-sib, half-sib and parent-offspring) were avoided and generations were over-lapping. In 1990 the population was characterised as having light mature body weight, small litter size and slow growth rate (Opoku and Lukefahr, 1990), although typical for local populations of rabbit found in both arid and tropical geographic regions of the world (El Amin., 1978; Finzi *et al.*, 1988; Lukefahr, 1988). However, by 1990 the NRP population had been downsized to as low as 30 and 150 breeding bucks and does, respectively, due to budget cuts from the GOG.

This population continues to exemplify remarkable phenotypic diversity in both qualitative (e.g. coat colour and pattern) and quantitative characters (e.g. adult weight, body conformation and litter size), as would be expected for a population with such a heterogeneous background. Production trait statistics, based on analyses of NRP data, are shown in table 2. Whereas litter survival rates are high from birth to 90 days of age, means for litter size are small, which may reflect the light mature body size of the stock (2 667 and 2 350 g for does and bucks) and (or) the adverse tropical environment. Within-trait variation was largest for litter size characters, intermediate for litter weights and survival rates and smallest for individual 90-day body weight.

Genetic characterisation project

In 1989 a research project directed by the author, entitled "Development of a Synthetic Tropical Rabbit Breed", involved a collaborative venture between Alabama Agricultural & Mechanical University (AAMU) and the NRP, Ministry of Agriculture. In the same year, the USAID funded project was formalised via a Memorandum of Understanding. The research programme was aimed at genetically characterising the composite

Table 2. Production Trait Statistics for the National Rabbit Project Population in Ghana.

	Descriptive Statistics*			
Trait**	Mean	SEM	PSD	CV
Total litter size born	4.90	0.189	1.72	35.2
Percentage live births	98.2	0.79	7.2	7.3
Litter wt at 21 d, g	881	21.3	195	22.1
Litter size weaned (56 d)	3.81	0.147	1.34	35.2
Litter wt at 56 d, g	2596	73.6	618	23.8
Preweaning survival rate, %	83.0	1.86	16.8	20.2
Individual wt at 90 d, g	1355	23.8	202	14.9
Postweaning survival rate, %	87.8	2.06	18.8	21.4

*N = Data consisted of 92 litters born with 313 kits surviving to 90 d of age.
**Mean = least-squares mean, SEM = standard error of the mean, PSD = phenotypic standard deviation, and CV = co-efficient of variation. The model included sires (n=25), batch (n=4), and the residual term (df=64).
Source: Opoku and Lukefahr (1990).

population, which by this time was considered as a straight-bred population. In addition, AAMU sponsored a post-graduate, M.S. student, who specialised in rabbit breeding and genetics (Atakora 1992). In 1992 the candidate returned to the NRP, as the NRP director, to provide project leadership and genetic expertise.

According to the research study protocol, the NRP stock was randomly grouped into sire and dam families in a hierarchical experimental design (e.g. dams were nested within sires). All matings were made at random except for close relatives. On a within-litter basis (n=92 litters), offspring produced in the first generation were randomly selected as parents to produce progeny for the second generation. As an indicator trait of the heterogeneous population, data on individual 90-day body weight were collected over two consecutive generations (birth years were 1989 and 1990) from 687 rabbits representing 61 sire and 194 dam families. Paternal half-sib estimates of heritability for first and second generations were 0.41 ± 0.19 and 0.43 ± 0.18 (Lukefahr *et al.*, 1992). These estimates also confirm the heterogeneous nature of the NRP population because literature estimates of heritability are generally lower. In agreement, Moura *et al.* (1997) reported heritability of 0.48 for average daily gain (56 to 84 days) involving 1 446 rabbits from a four-breed composite population in Hawaii.

In addition, based on the assumption of an additive genetic model, table 3 presents fractions (upper limit) of common litter variance (V_{EC} = 0.16 and 0.18) and residual, within progenies environmental variance (V_{EW} = 0.43 and 0.39) for first and second generations, respectively, using methods described by Falconer and Mackay (1996). Alternatively, by relaxing the former model, upper limit estimates of dominance genetic variance (V_D = 0.57 and 0.52 in first and second generations) were obtained by setting V_{EW} to zero (Table 3). Of course, it is quite unlikely that V_{EW} was zero in this population. In the latter case, corresponding lower limit estimates of common litter variance (V_{EC} = 0.02 and 0.05 in first and second generations, respectively) were calculated. Perhaps the most useful knowledge gained from the variance component analysis was the high heritabilities and the narrow range of estimates for the common litter variance of 0.02 and 0.16 for generation one, and 0.05 and 0.18 for generation two, respectively. Common litter and (or) maternal effects appeared to be small in full-sib families.

In retrospect, a conservative estimate of the number of breeding males and females could be 30 and 150 animals. This would relate to a projected effective population size of 100 animals and a maximum rate of inbreeding of 0.5 percent per generation. To determine the extent that genetic response for 90-day body weight could or might have occurred, the following calculations are made. On average, a breeding doe would be expected to produce eight litters over a production lifespan of two years. Each litter would contain five offspring. Assuming equal sex ratio, this would relate to 1 / 20 or 5 percent doe selection rate. To account for attrition and culling,

Table 3. Within-generation estimates of causal components of variance for 90-day body weight (g) from the National Rabbit Project in Ghana, according to genetic model.

		Causal variance components*			
Model**	Generation	V_A	V_D	V_{EC}	V_{EW}
I	First	0.41	0.00	0.16	0.43
	Second	0.43	0.00	0.18	0.39
II	First	0.41	0.57	0.02	0.00
	Second	0.43	0.52	0.05	0.00

* Components expressed as fractions of total phenotypic variance.

** Model I assumes an additive genetic (V_A) model with upper limits for common (V_{EC}) and residual (V_{EW}) environmental effects, whereas Model II assumes an additive and dominance (V_D) genetic model with upper limits being estimated for V_D and lower limits for V_{EC} (V_{EW} set to zero).

Source: Lukefahr *et al.* (1992).

a 10 percent replacement rate is figured (i_f = 1.755). If breeding males remained in the herd for one year, on average, then 150 does producing 600 litters would relate to 1 500 male offspring. Selecting 30 male offspring would be a selection intensity of 2 percent. To be more conservative, the 2 percent figure is doubled (i_m = 2.154). The average selection intensity is 1.955. Heritability was estimated at 0.42 and the phenotypic standard deviation was 221.9 g. Generation intervals for males and females are figured at 1.5 and 1 year of age, respectively (age at first mating is six months). Using phenotypic, mass selection, the selection accuracy is the square root of heritability, which is 0.65. Predicted genetic response per year is 146 g [10.8 percent of the population mean of 1 355 g (Lukefahr and Opoku, 1990)]. Hence, it appears that the NRP had (has) the opportunity to realise rapid genetic improvement if this is deemed as the breeding goal.

Appropriateness of cross-bred stock for farmers

As elucidated by Lukefahr (1998), the maintenance of a heterogeneous population ("non-standard breed") which is locally adapted may have real merit in adverse environments, despite the conventional wisdom that local rabbit populations in LDC are genetically inferior. A high degree of heterozygosity or heterosis might be important for fitness-related characters (e.g. fertility and survival) as a means of eventual local adaptation (Falconer and Mackay, 1996). Obviously, the NRP population, in the breeding history and (or) conditions previously specified (e.g. foundation of some sixteen breeds [including a local breed], production of several F_1 lines and inter-crossings of these lines), should be highly heterozygous with a preponderance of desirable candidate genes for adaptation and production traits. Theoretically, the level of retained heterosis could be as high as 94 percent if all sixteen original breeds contributed equally to the composite population. Further, it is plausible that multiple alleles or polymorphism at relatively more loci than as found in other populations, many genes being found at close to intermediate frequencies, may largely account for the higher heritability (0.41 and 0.43) for 90-day body weight than is generally reported in the literature. In addition, genetic progress is likely to have occurred at two levels: first, that immediately realised from initial cross-breeding (infusion of genes for production), and second, from subsequent, within-population selection involving, no doubt, both artificial and natural selection (producing desirable gene combinations for adaptation and production). By the early to mid 1990s, it was considered that the NRP population was essentially a locally adapted, straight-bred population appropriate for small-scale farmers in low input conditions in Ghana.

From the perspective of the small farmer, the ultimate user and steward of rabbit genetic resources, NRP stock is observed to be prolific, growth and tractable, which explains their popularity and high demand. In addition, these rabbits appear to be anatomically and physiologically sound in many regards as these qualities presumably pertain to relative efficiency of reproduction, growth, longevity, etc. from a genetic adaptation point of view. For example, such qualities include lengthy ears, thin fur density, large body surface area, wide foot pads, good fertility even during hot months and high forage intake capacity. These non-traditional characters may have real merit as potential selection criteria and may have been the basis for indirect genetic gains achieved through selection for increased 90-day body weight. This breeding philosophy varies from the traditional selection approach involving measures on production traits (e.g. litter size, growth rate and carcass yield). More research in this area is certainly warranted.

Unfortunately, this novel straight-bred population has yet to be formally inventoried into FAO data banks. In general, locally adapted populations as opposed to exotic or upgraded straight-breds may be more amenable for inclusion in genetic resources data banks and for effective conservation. This approach is in contrast to frequently observed attempts in other countries to reintroduce and conserve exotic straight-breds or regular outcrossed lines at breeding stations which may well not be adapted or appropriate for small farmers. As a composite breed, only *inter se* matings are necessary for farmers to maintain the genetic integrity of this population, largely provided that numbers remain adequate.

Fortuitously, through stock utilisation in villages in subsistence conditions, small farmers have played a major role, albeit unplanned, in effectively conserving this novel rabbit population. For many farmers, stock has been purchased only once. Other farmers have purchased stock even on a regular basis. However, in either case there has been no known re-introduction of stock from farmers into the NRP population. The village cooperative breeding scheme simply has involved a two-tier structure. The NRP population is managed at both levels, therefore. Since farmers mate their rabbits as straight-bred animals, the breeding system is sustainable from a genetic management standpoint considering the large number of rabbits (e.g. tens of thousands) that have been distributed and maintained by farmers across villages. Fortunately, this figure certainly far exceeds the estimate of the effective breeding population size of 100 animals at the NRP. Hence, the breed has largely been genetically conserved and maintained by farmers under low input systems.

Conclusions

Since 1972 a very conservative estimate of over 37 000 Ghanaians having been directly assisted by the NRP through stock provision, training, visitation, etc., has been reported (Opoku and Lukefahr, 1990). This success, in part, is attributable to the direct support of the GOG, the dynamic leadership and expertise of the NRP founder, Mr N. Mamattah and later on to formal NRP staff development and graduate training in breeding and genetics. From a genetic standpoint, the success is also due to the suitability of appropriate rabbit breeding stock from the NRP which, for nearly 30 years now, has continued to be distributed to and in high demand by farmers.

In retrospect, some of the original breeds representing exotic introductions to the NRP (e.g., Alaskan, Crème D'Argent and French Lop) might have been excluded since they are fancy breeds, they would have offered few desirable genes for production. Also, the imported breeds could possibly have been procured from more similar, tropical environments to have enhanced the chances for survival and (or) genetic adaptation.

It would be desirable if the NRP was to continue measuring conventional production traits (e.g. body weight and litter size) but also anatomical and physiological characters (e.g., body surface area, ear length, forage intake capacity and fur density) which may be more closely connected to a genetic adaptation. Knowledge on the extent that these traits are genetically correlated would be very useful and of ultimate benefit to farmers.

In addition, it would also be useful to compare the present NRP straight-bred population to local rabbits (if still to be found) for traits of importance to small-scale farmers. From a genetic management standpoint, it would be desirable to allow outstanding animals from farmers to enter the NRP nucleus population. With an estimated effective population size of only 100 animals, the NRP needs not only to allow genes from outstanding animals to be infused, but also to at least double the breeding population size at the NRP. Of course, the former will require close collaboration between NRP staff and farmers, clearly defined breeding objectives, performance recording and genetic evaluation systems, etc. The latter will require an increase in staff, feed and supplies and operation budget.

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