

Analysis of Alternative Pure-breeding Structures for Sheep in Smallholder and Pastoral Production Circumstances in the Tropics

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Abstract

The key issue in this study was to technically compare, through stochastic simulation, different breeding programmes that vary in the level of interaction between breeders and producers. The breeding structures considered were: (i) a single closed nucleus providing seed-stock to village flocks, (ii) a group of commercial flocks running a co-operative ('ram circle') breeding programme with no nucleus, (iii) an interactive two-tier open nucleus breeding scheme, comprising a nucleus and a commercial tier - the best males are used within the nucleus while the remainder migrate to the commercial flocks, with no female migration, and (iv) as scheme iii but with female migration between tiers. For the latter two schemes, 100% of the nucleus animals are distributed over village flocks every 3 years. The nucleus is then replaced by a new batch of selected males and females from the village flocks obtained through 'interactive cycling screening', based on 'picking the best phenotype' in the commercial flocks. Single trait selection was considered, and based on estimated breeding value, using either best linear unbiased prediction (BLUP) or the individual's phenotype as a deviation from contemporaries in the same flock, year and season. The results showed that genetic merit increased slightly and inbreeding decreased significantly with increase in nucleus size. For instance, with BLUP selection and trait measurement on both sexes, and first record established at year 2, a nucleus size of 100 dams with 50 dams mated to each sire resulted in genetic merit of 0.118 units and an average inbreeding coefficient of 0.119 while that with 500 dams gave a response of 0.134 with an average inbreeding coefficient of 0.037. Running one closed nucleus had a 6-24% advantage over a 'ram circle' in terms of genetic gain. Decreasing the dam to sire ratio was a simple way to avoid inbreeding in breeding schemes of small size, with very little compromise towards genetic gain or even an increase in the longer term. Relative to a two-tier nucleus (scheme i), cyclic screening of commercial animals for use in the nucleus gave an almost optimum genetic response, while the villagers acquired superior breeding stock in return as an incentive to participate in genetic improvement. Participation of farmers offers them a sense of ownership of the breeding programme, and is likely to make it more sustainable in the long-term. This study provides insight into the advantages and disadvantages of designed breeding structures, especially the 'interactive cyclic' breeding schemes, which should be useful in deciding breeding programmes to adopt for sheep in developing countries in the tropics.

Keywords: Sheep, Breeding Structures, Selection, Tropics

1. Introduction

Sheep play an important role in the livelihood of many people in the tropics, mainly through meat production (Carles, 1983; Gatenby, 1986; Kiwuwa, 1992; Kosgey, 2004), and they have potential for greater contribution through better management and genetic improvement (Kosgey et al., 2002; Kosgey & Okeyo, 2007). Traditional minimal-input systems with indigenous animal breeds predominate, mainly in the arid and semi-arid areas, which practice pastoral-nomadic systems of livestock production (Gatenby, 1986; de Leeuw et al., 1991; Kiwuwa, 1992; Kosgey & Okeyo, 2007). A smaller proportion of small ruminants per household are traditionally kept in humid, semi-humid and highland eco-zones, where sedentary agricultural and agro-pastoral production systems are practiced (e.g., Kiwuwa, 1992).

The traditional production systems may not render organized national or regional genetic improvement of productive traits of small ruminants feasible. Village breeding programmes are, therefore, predominant in the tropics and have been defined by Sölkner et al. (1998) as those breeding programmes carried out by communities of smallholder farmers (villagers), often at subsistence level. Under smallholder production systems in the agro-pastoral areas, effective small ruminant conventional breeding methods are constrained by communal grazing, small flock sizes, single-sire flocks, lack of systematic animal identification, inadequate animal performance and

pedigree recording, low levels of literacy and organizational shortcomings (Kiwuwa, 1992; Kosgey & Okeyo, 2007). In addition to the factors constraining successful small ruminant breeding strategies in smallholder production systems, apart from small flocks and probably single-sire flocks, pastoral flocks face a problem of mobility. The infrastructure necessary for collection of reliable pedigree and performance data does not exist to set up a breeding programme involving the populations maintained by the mobile pastoralist communities (Franklin, 1986; Kiwuwa, 1992; Kosgey & Okeyo, 2007). Consequently, strategies for genetic improvement that overcome these problems need to be considered. In this regard, nucleus schemes have been proposed as a good strategy for genetic improvement of livestock in developing countries (Hodges, 1990; Jasiorowski, 1990; Kiwuwa, 1992; Kosgey, 2004). Depending on the complexity and requirements of the breeding programme, a nucleus scheme can have different numbers of tiers and migration policies. Van der Werf (2000) has summarized the roles of the different tiers in a livestock breeding structure. Generally, the central nucleus and multiplier flocks generate sires for distribution to commercial farmers, i.e., smallholders and pastoralists. However, a crucial point for the successful implementation of a breeding scheme is adequate interaction between the nucleus and commercial sectors, in a technical as well as socio-economic sense.

In this study, a nucleus is defined as a unit with several breeding males. The best (“elite”) males in the nucleus population in each generation, and with female migration, the best females in the whole population are used in the nucleus to produce the best offspring. A breeding flock is considered as a breeding unit around one breeding male. At the village level, a private ‘flock’ might consist of only a few animals, but a group of smallholders within one village could commonly share a breeding male. The breeding male is then obtained either from the nucleus, or from another flock, i.e., a group of smallholders sharing a breeding male.

One option other than a central nucleus is to run a co-operative ‘ram circle’ breeding programme among a number of larger commercial groups. According to Kiwuwa (1992), once recording has improved on the part of the farmers, co-operative breeding schemes based on central nucleus flocks without associated multiplier flocks could be adopted. However, this is still quite infeasible in most production systems in the tropics. Information on the principles and experiences of co-operative breeding programmes can be found in a number of studies (e.g., Dodd et al., 1982; McMaster, 1982; Parker and Rae, 1982; Peart, 1982; Steine, 1982; Williams, 1982; Kiwuwa, 1992; Ponzoni, 1992; Bett et al., 2012), and many of these relate to tropical scenarios.

A third option is an ‘interactive cyclic’ scheme, where breeding stock from the nucleus is regularly interchanged with village stock. There appear to be no previous studies on ‘interactive cyclic’ screening schemes. Such schemes may be an appropriate strategy for village-based breeding programmes in agro-pastoral and pastoral-nomadic production systems because it involves the village farmer community more intensively but with minimal recording required in the commercial flocks, which would otherwise be a big challenge due to the various bottlenecks that would be encountered with data collection and analysis in these production systems.

The aim of the current study was to examine more interactive breeding programmes, and to technically compare, through simulation, alternative sheep pure-breeding schemes. The interaction of nucleus schemes with commercial flocks, in particular the interaction between breeding flocks and commercial farmers was studied. The parameters used to compare the schemes studied were the obtained genetic improvement for merit (ΔG) and the average inbreeding coefficient (F). The effects of nucleus size and dam to sire ratio, and cyclic screening of animals were evaluated. Incentives for producers to participate and contribute to the breeding programme were also considered.

2. Research Materials and Methods

Stochastic simulation was used with 100 replicates of a breeding population with overlapping generations simulated for 10 years. All the calculations related to genetic merit are in units of phenotypic standard deviation (SD). One SD is generally equal to 10-20% of the mean. Therefore, a genetic response of 1.00 in 10 years reflects an annual genetic change equal to 1-2% of the trait mean. The calculated rates of genetic gain (ΔG) account for the effect of selection and inbreeding on genetic variance (Bulmer, 1980).

The breeding structures considered were: (i) a two-tier breeding scheme, comprising a single nucleus and a commercial tier. The nucleus was closed and there was no specific mating strategy applied (i.e., there was random mating of selected males and females), (ii) a group of commercial flocks running a co-operative (‘ram circle’) breeding programme with no nucleus - males selected within each flock were used in another flock while females were selected but did not migrate between flocks, (iii) an interactive two-tier breeding scheme, comprising a nucleus and a commercial tier (Figure 1 below) - the best males were used within the nucleus while the remainder migrated to the commercial flocks, with no female migration, and (iv) as scheme iii but with female migration between tiers. A commercial flock is defined as a breeding unit around one male, potentially comprising a group of smallholders or pastoralists within one village.

In schemes iii and iv, there was cyclic screening of commercial animals for the nucleus every 3 years (Figure 1). Screening was based on ‘picking the best phenotype’ in the commercial flocks and using this in the nucleus. The screened animals from commercial flocks were assumed to have no pedigree record, but had an

own performance record obtained from simple recording introduced earlier in the flock. A lower accuracy of selection (equal to the square root of half of the heritability) was then used, which makes it more realistic for smallholder and pastoral production circumstances in the tropics. Although the result is not a formal measurement, it was treated as such in the simulation. Both sexes were selected at the age of 7 months.

Sample animals from village flocks

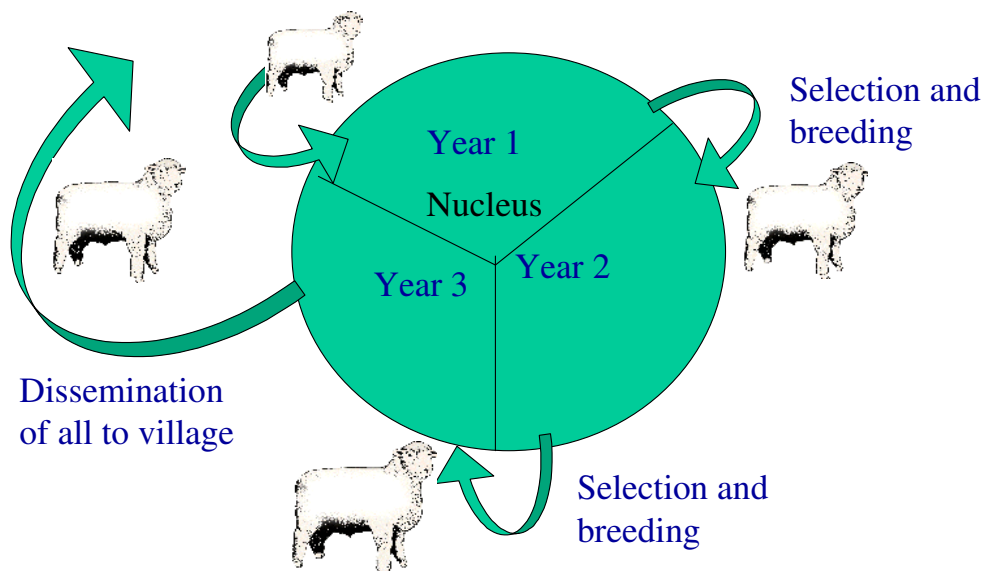


Figure 1. Cyclic screening of animals in the 'interactive cycling' schemes (i.e., scheme iii and iv)

Selection in the nucleus was based on truncation using BLUP estimated breeding values (EBVs) as criterion and, therefore, optimizing selection across age classes. Pedigree information was absent for commercial-born animals in the nucleus. Animals not selected as nucleus parents were selected for dissemination to the commercial flocks. Only natural mating was considered. It was assumed that the sire to dam mating ratio was the same in nucleus and commercial flocks. In all cases, survival probabilities decreased by 10% each year increase of age starting at 90% in year 1 (Kosgey et al., 2003). Age at drop of first progeny was assumed to be 2 years. The phenotype was recorded during the second year on both sexes with selection on traits that are measurable early in life and on both sexes, for example, survival traits (e.g., pre-weaning survival) and lamb birth weight. Additionally, a trait recorded later in life (3 years of age) on females only was simulated, which represents traits like reproductive traits (e.g., litter size and lambing frequency) and mature ewe weight.

In the present study, single trait selection was considered with a heritability of 0.25 and based on estimated breeding value (EBV), using BLUP or the individual's phenotype as a deviation from the contemporaries in the same flock, year and season. When only females were measured, and with selection on phenotype, males were selected based on $0.5 \cdot \text{EBV}(\text{dam})$. Animals could be selected as parents irrespective of age or availability of records. For older animals, EBVs could include progeny information. However, progeny testing was not a pre-requisite for selection, but selection with BLUP could partly be based on progeny information. Genetic response was calculated from the mean breeding values over the simulated period per year. Inbreeding was calculated using the Meuwissen & Luo (1992) algorithm as modified by Quaas (1995).

3. Results

3.1. Effect of nucleus size and dam to sire ratios

Table 1 below presents the results of closed nucleus versus 'ram circle' breeding schemes, and shows the effect of nucleus size, and dam to sire ratios on the rate of genetic response (ΔG) and the average inbreeding coefficient in year 10 (F_{10}). This refers to variations of scheme i and ii. With an increased nucleus size, ΔG increases slightly whereas F decreases significantly. For instance, with BLUP selection and trait measurement on both sexes, and first record established at year 2, a nucleus size of 100 dams with 50 dams mated to each sire resulted in ΔG of 0.118 units and F_{10} of 0.119 while that with 500 dams gave a response of 0.134 with F_{10} of 0.037. The standard errors (s.e.) of ΔG reduced with increase in the size of the scheme, indicating less variation in response when the scheme was larger. For example, s.e. reduced from 0.024 to 0.014 units when the nucleus size was increased from 100 to 500 dams. A similar effect was found in a 'ram circle'. However, ΔG for a 'ram circle' was little affected by the scheme sizes tested under phenotypic selection. Generally, response to selection was higher if a trait could be measured early in life and on both sexes. For instance, with a population of 500 dams and BLUP selection, ΔG were 0.134 and 0.111 units for the nucleus and the 'ram circle' schemes, respectively, when trait

measurement was at year 2 and both sexes recorded with 50 dams mated to each sire. If trait measurement was at year 3 and on females only, the corresponding responses were 0.080 and 0.066, which were, correspondingly, about 60% and 41% lower.

When more sires were used for a given flock size in both the nucleus and ‘ram circle’ schemes, ΔG decreased slightly but F_{10} decreased drastically. For instance, in a nucleus of 100 dams and phenotypic selection in both sexes with trait measurement at year 2, units for ΔG were 0.100 and 0.097 for 50 and 20 dams per sire, respectively. The corresponding F_{10} values were 0.118 and 0.061. The ‘worst case’ scenario in terms of ΔG was when trait measurement was on one sex only with a smaller nucleus size. This was best illustrated by a nucleus scheme of 100 dams and 50 dams mated to each ram. In this case, ΔG was 0.067 and 0.051 units for BLUP and phenotypic selection, respectively. The corresponding s.e. were 0.026 and 0.030, with respective F_{10} values of 0.091 and 0.123, and were among the highest. This suggests a higher variation in response in phenotypic selection.

Table 1. Responses per year (ΔG) in units of phenotypic standard deviation, their standard errors (s.e.) and average inbreeding (F_{10}) after 10 years of BLUP or phenotypic selection in closed nucleus or ‘ram circle’ breeding schemes of varying size^{a,b}

Scheme	No. of dams	No. of sires	Trait measurement	BLUP selection			Phenotypic selection		
				ΔG	s.e.	F_{10}	ΔG	s.e.	F_{10}
Nucleus	50	5	Year 2/both sexes	0.096	0.017	0.067	0.088	0.020	0.060
				0.099	0.014	0.036	0.091	0.017	0.032
				0.118	0.024	0.119	0.100	0.026	0.118
				0.129	0.017	0.064	0.107	0.022	0.055
				0.134	0.014	0.037	0.112	0.014	0.030
	100	2	Year 3/females only	0.109	0.017	0.063	0.097	0.022	0.061
				0.120	0.010	0.015	0.103	0.010	0.013
				0.145	0.017	0.066	0.120	0.020	0.056
				0.067	0.026	0.091	0.051	0.030	0.123
				0.080	0.014	0.027	0.055	0.014	0.032
‘Ram circle’	2	Year 2/both sexes	0.069	0.020	0.046	0.050	0.020	0.060	
			0.070	0.010	0.011	0.050	0.010	0.013	
			0.107	0.024	0.089	0.088	0.026	0.117	
			0.112	0.014	0.034	0.099	0.017	0.032	
			0.111	0.010	0.028	0.099	0.010	0.020	
‘Ram circle’	2	Year 3/females only	0.096	0.017	0.036	0.089	0.020	0.034	
			0.097	0.010	0.027	0.089	0.010	0.019	
			0.060	0.026	0.084	0.051	0.026	0.112	
			0.066	0.010	0.026	0.052	0.014	0.021	
			0.056	0.017	0.036	0.046	0.017	0.044	
‘Ram circle’	2	Year 3/females only	0.058	0.010	0.023	0.046	0.010	0.015	
			0.058	0.010	0.023	0.046	0.010	0.015	

^aAge at drop of first progeny is 2 years.

^bBased on 100 replicates.

Responses from closed nucleus schemes tended to be higher than those from a ‘ram circle’ scheme of the same size. For instance, under phenotypic selection, a scheme of 250 dams with 50 dams mated to each sire had ΔG of 0.107 units for the nucleus and 0.099 for the ‘ram circle’. The latter scheme had lower F_{10} . Generally, ΔG was about 6-24% less for the ‘ram circle’ schemes compared to closed nucleus schemes. However, the responses tended to fluctuate less with variation in the size of the ‘ram circle’ scheme for a given dam to sire mating ratio. BLUP selection resulted in better ΔG than phenotypic selection for nucleus schemes of the same size but slightly higher F_{10} except with selection on traits measured late on one sex. This was surprising, as more inbreeding was expected with BLUP. The fact that males were selected based on $0.5 \times EBV(\text{dam})$ might have caused this occurrence. Inbreeding became worse when the nucleus size was smaller and phenotypes were on

females only (i.e., sires were selected based on their dam's record), and measured after selection as BLUP uses more information from relatives in such cases.

3.2. Effect of cycling screening and migration of animals

Table 2 below gives a comparison between a two-tier system (scheme i) and an 'interactive cyclic' screening strategy when only males were migrated to the village flocks (schemes iii), and when both males and females were distributed from nucleus flocks (scheme iv). The figures presented for the commercial tier refer only to the mean of the animals going to commercial flocks. Genetic trends are illustrated in Figures 2 and 3 below. In the two-tier system, the nucleus was basically closed, and excess males were distributed over commercial flocks. The nucleus was set up initially by selecting the best males and females from commercial flocks (based on a lower accuracy equal to the square root of half of the heritability). In the 'interactive cyclic' screening schemes, all nucleus animals were distributed over village flocks every 3 years and the nucleus was replaced by a new batch of selected males and females from the village flocks (Figure 1).

Table 2. Responses (ΔG) in units of phenotypic standard deviation in the nucleus, genetic lag (GL) between the nucleus and commercial tier and average inbreeding (F) in a 2-tier system (scheme I) and 'interactive cycling' screening strategies (scheme III and IV) based on BLUP selection over a 15-year period^{a,b,c}

Year	Single 2-tier nucleus scheme				'Interactive cycling' screening scheme				ΔG^c	GL ^c	s.e.	F ^c
	ΔG	GL	s.e.	F	ΔG^d	GL ^d	s.e.	F ^d				
1	0.373	0.373	0.036	0.000	0.369	0.369	0.032	0.000	0.352	0.352	0.035	0.000
2	0.388	0.388	0.039	0.000	0.365	0.365	0.035	0.000	0.349	0.349	0.039	0.000
3	0.676	0.256	0.041	0.010	0.680	0.294	0.035	0.011	0.669	0.270	0.042	0.010
4	0.758	0.314	0.042	0.019	0.749	0.033	0.055	0.000	0.747	-0.048	0.055	0.000
5	0.938	0.384	0.044	0.030	1.008	0.471	0.037	0.018	0.992	0.406	0.050	0.015
6	1.054	0.457	0.046	0.042	1.126	0.498	0.055	0.012	1.122	0.410	0.057	0.011
7	1.195	0.519	0.051	0.055	0.974	-0.172	0.054	0.000	1.053	-0.095	0.073	0.000
8	1.322	0.590	0.049	0.068	1.415	0.671	0.055	0.027	1.410	0.530	0.060	0.018
9	1.459	0.650	0.060	0.080	1.452	0.668	0.055	0.019	1.468	0.550	0.058	0.013
10	1.589	0.714	0.057	0.094	1.146	-0.253	0.055	0.000	1.257	-0.204	0.066	0.000
11	1.725	0.794	0.062	0.109	1.706	0.793	0.057	0.041	1.707	0.635	0.063	0.019
12	1.829	0.823	0.059	0.121	1.719	0.855	0.057	0.030	1.737	0.672	0.062	0.015
13	1.965	0.891	0.062	0.137	1.204	-0.366	0.062	0.000	1.404	-0.267	0.064	0.000
14	2.074	0.943	0.062	0.149	1.990	0.965	0.060	0.057	1.917	0.693	0.062	0.020
15	2.208	1.003	0.063	0.162	1.964	1.0647	0.057	0.047	1.926	0.750	0.062	0.017

^aThe nucleus size is 250 dams and screening on the offspring of 250 commercial animals. ^bAge at drop of first progeny is 2 years, and first record is established during second year, with both sexes recorded. ^cFifty dams are mated to each sire. ^dMigration of sires only from the nucleus to commercial flocks (scheme iii), and ^eMigration of both sires and dams allowed (scheme iv).

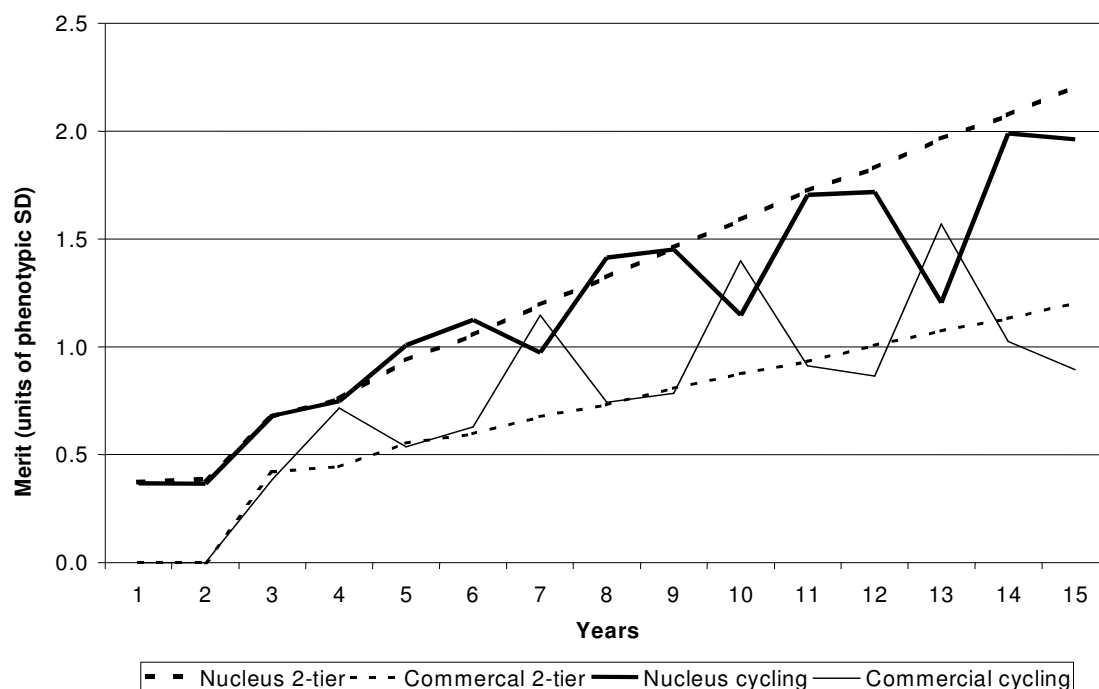


Figure 2. Genetic improvement in a nucleus and commercial flocks for a two-tier system (scheme i) and for a

system with 3-yearly cyclic screening of commercial flocks to replace the nucleus, and only males were migrated to the commercial flocks (scheme iii). The nucleus size was 250 dams and screening on the offspring of 250 commercial animals, with 50 dams mated to each sire. Age at drop of first progeny was 2 years, and first record was established during second year, with both sexes recorded.

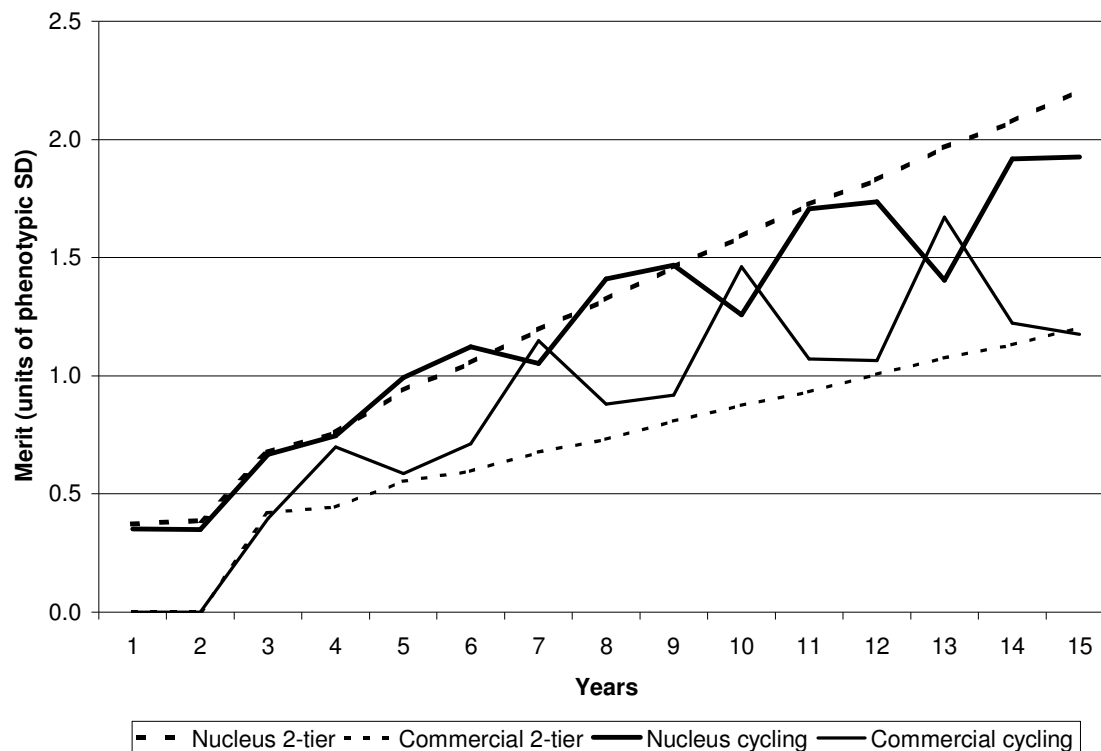


Figure 3. As Figure 2, except both sexes were migrated to the commercial flocks (scheme iv) Generally, the genetic trends in the three schemes (i, iii and iv) were quite similar over time (Figures 2 and 3). As expected, the commercial flocks in the two-tier system (scheme i) genetically lagged behind the nucleus flocks. However, F increased to unacceptably high levels in such a scheme. In the ‘interactive cyclic’ screening scheme, the genetic mean fluctuated over time and the nucleus pulled ahead of the commercial population except when a new batch of village flocks was brought in. In that case, the commercial population got a genetic lift. For example, in scheme iii in year 10, the commercial flock was about 22% ahead of the nucleus genetically. In the subsequent year, the genetic merit of the nucleus was about two times that of the commercial population since year 0. The reasons for the slow down of genetic trend after year 10 and the negative response in year 12 in the commercial tier are not clear.

The levels of F in the ‘interactive cyclic’ schemes also fluctuated but remained very low and were actually zero whenever a new batch of animals was ‘picked’ for the nucleus from the village flocks (Table 2). At year 15, for instance, F was just above 4% in scheme iii. However, F was biased downwards because the pedigree of commercial animals was not available and, therefore, not used for calculation of F. Generally, an ‘interactive cyclic’ screening scheme that allowed migration of both males and females from the nucleus to the commercial flocks (scheme iv) resulted in slightly higher ΔG for commercial flocks compared with the scheme that allowed migration of males only (scheme iii) and, in the long-run, F was lower. The variation in response was slightly higher for the scheme that allowed migration of both sexes. With BLUP selection, the commercial flocks had a genetic lag that was, on average, about two generations behind that of the nucleus when only males were migrated. Genetic gains in ‘interactive cyclic’ schemes compared favourably in some instances with the two-tier scheme (scheme i). These schemes got a genetic lift when they received animals from the nucleus while the nucleus could or could not drop depending on the breeding values of the ‘picked’ animals from the commercial flocks vis-à-vis those they would replace in the nucleus (Figures 2 and 3).

4. Discussion and conclusions

Structured breeding systems are important for the genetic improvement of sheep in developing countries in the tropics. The aim of the current study was to determine the benefit of different pure-breeding nucleus schemes interacting with commercial flocks. The key issue was to technically examine different breeding programmes that vary in the level of interaction between breeders and producers under smallholder and pastoral production

circumstances in the tropics.

Genetic improvement can be obtained from male and female selection, with the first being the major contributor to genetic improvement. It is important from the outset to bear in mind that possible rates of genetic improvement depend on the time that the trait can be measured and whether or not the trait can be measured on both sexes or on females only. A nucleus breeding structure is a convenient start for many breeding programmes as trait measurement, selection and mating are easier to manage (Hodges, 1990; Kiwuwa, 1992; van der Werf, 2000). It is not worth including all animals of a population in the active part of a breeding programme due to measurement and recording costs, and lack of proper control (Kingham et al., 2000). It is recommended that nucleus breeding programmes for sheep in developing countries evolve towards an open nucleus where the best females from the commercial population can be migrated up for breeding in the nucleus (Jasiorowski, 1990). The dilemma is how to effectively organize breeding schemes involving farmers at the village level, how to record such flocks and to monitor progress (Osinowo & Abubakar, 1988). To involve farmers, it is advisable to back the breeding programme with an effective extension service for maximum effect. Before initiation of the selection programme, it should be preceded with several years of extension work to train the farmers and boost their experiences and skills in sheep production techniques (e.g., Yapi-Gnoare, 2000). During that period, farmers should be made aware of the benefits derived from the recording activity (Moioli et al., 2002).

It was shown in the current study that nucleus size influenced both the rate of genetic response (ΔG) and the predicted average inbreeding coefficient (F). Genetic merit increased slightly with increase in nucleus size while F decreased (Table 1). Garrick et al. (2000) observed a similar trend with regard to ΔG and reported increases in costs of genetic improvement when the nucleus size was increased. Costs of running the schemes were not considered in the current study.

A genetic improvement programme from a small nucleus flock of a few animals can give an unacceptably high level of inbreeding. However, this depends on the number of males used (Table 1). Increasing the number of males reduces F at very little expense of ΔG due to lower selection differential. It was shown in the present study that it is still possible to make greater ΔG even with smaller flocks. For instance, a nucleus with 50 dams and 5 sires gave ΔG that was only 12% lower compared to a nucleus of 100 dams and 50 sires, and 28% less than the response from a scheme of 500 dams and 10 sires with BLUP selection (Table 1). The differences in ΔG tended to be lower with phenotypic selection. However, F_{10} was higher for the smaller scheme. Other studies have recommended that, for a single nucleus-breeding flock, at least about 500 breeding females are needed (e.g., Turner, 1982; Udo, 1994). A smaller nucleus is permitted if it is started up with periodic recruitment of breeding males from commercial flocks, as effectively a much larger founder population is used for the nucleus, or if proper use is made of optimal contributions to help control inbreeding (Meuwissen, 1997).

There was some advantage of running one closed nucleus over a 'ram circle'. The rate of genetic improvement was about 6-24% less for the 'ram circle' (Table 1). However, 'ram circle' breeding programmes can, to some extent, be useful when selection can be based on an individual's phenotype in both sexes. The difference between the nucleus and the 'ram circle' schemes increased with selection on a late trait in one sex only compared to an early trait in two sexes.

BLUP selection leads to significantly more genetic gain than selection on individual phenotype but the increased gain is accompanied by more inbreeding. Using information from related animals increases the chance of co-selection of members of the same (good) family (Belonsky & Kennedy, 1989). Dynamic selection rules (e.g., Wray & Goddard, 1994; Meuwissen, 1997) have been developed that maximize selection response while limiting the rate of inbreeding. At the same rate of inbreeding, Meuwissen & Sonesson (1998) found that the dynamic selection method obtained up to 44% more genetic gain than truncation selection on BLUP breeding values. The advantage of the dynamic selection method over BLUP selection decreased with increasing population size and with less stringent restriction on inbreeding.

Generally, a two-tier closed nucleus scheme supplying seed-stock to commercial flocks (i.e., scheme i) was better than the 'interactive cyclic' screening scheme in terms of genetic gain (Table 2). There is better trait measurement and selection in the nucleus and, therefore, an increased advantage over the 'interactive cyclic' schemes. In the latter schemes, the commercial tier got a genetic boost only when they received improved animals from the nucleus and, thereafter, dropped again drastically. However, there was generally still substantial genetic trend, close to the results of the two-tier nucleus scheme (scheme i) (Figures 2 and 3). To avoid the drop, the commercial flocks could be encouraged to use their own rams for an extra year and wait until the nucleus catches up again. It is important to note that not all commercial animals are replaced by nucleus animals after the swap.

Opening the nucleus to the best animals from the commercial flocks would result in more sustained returns from selection in the commercial flocks due to more selection intensity and, therefore, more certainty that the best females (and males) are selected due to increased genetic variation in the next generation (Kingham et al., 2000). Open nucleus schemes provide an operational procedure for achieving greater genetic progress and more flexibility in meeting breeding objectives than does a closed nucleus (e.g., Parker & Rae, 1982). However,

measurement costs and logistics of data collection in commercial flocks are likely to be huge and not feasible in developing countries in the tropics and, therefore, the 'interactive cyclic' schemes proposed in the current study would be more practical as minimal recording is required.

As in other places (e.g., Garrick et al., 2000), the sheep industry structure in developing countries in the tropics is determined by the behaviour of breeders and farmers but there is often little individual incentive for these players to alter their practices despite overall benefit to the industry, plus the fact that they might not have the capital to buy breeding stock. Exchange breeding programmes where village flocks provide their best females and, in return, the villagers get breeding stock from the nucleus as an incentive to participate in genetic improvement, will likely make the breeding programme sustainable in the long-term. Such might be the basis of setting up 'interactive cyclic' schemes because they accord participation of the farmers in the operations of genetic improvement. Cyclic screening of commercial animals for use in the nucleus can give almost optimum genetic gains. Obviously, the nucleus will temporarily drop while the village flocks get a genetic lift. However, over time, ΔG is only slightly below that of a two-tier system (Figures 2 and 3).

Although the present study did not extensively examine ways to control inbreeding except the effect of different dam to sire ratios (Table 1), it is important to point them out due to the potential risk inbreeding poses in small breeding flocks in smallholder production circumstances commonly found in the tropics (e.g., Gatenby, 1986). Various methods have been proposed to reduce the rates of inbreeding in selection programmes while keeping genetic gains at the same level (for details see, e.g., Grundy et al., 1994; Wray & Goddard, 1994; Santiago & Caballero, 1995; Meuwissen, 1997; Kinghorn et al., 2000). These methods can be applied in combination with the genetic evaluation system. They require that the breeders are able to control mating strategies. It may be logistically difficult to control the mating strategy in smallholder and pastoralist traditional animal production systems in developing countries in the tropics, and manipulating the dam to sire ratio could be a simpler solution. Dynamic selection methods to control inbreeding rely on pedigree knowledge that is not often available in smallholder and pastoralist traditional animal production systems in the tropics. Therefore, in a breeding scheme, these dynamic rules and pedigree recording are only required for the nucleus population. Within the nucleus, the number of matings per breeding male can be restricted to limit the rate of inbreeding, while still maintaining optimal genetic progress. A village flock could use fewer males if they regularly import new males from neighbouring villages or the nucleus flock.

Reproductive rates can be manipulated by reproductive technologies such as artificial insemination (AI) for males, and multiple ovulation and embryo transfer for females (e.g., Kinghorn et al., 2000). The natural reproductive rate of ewes will limit their contributions, resulting in some fixed contributions (Meuwissen, 1997). Nevertheless, in extensive production systems such reproductive technologies are not always available or necessary (van der Werf, 2000). Use of AI is feasible (Rege, 1994; van der Werf, 2000), and it could be usefully applied for efficient dissemination of genetic improvement from the nucleus to commercial flocks (van der Werf, 2000). However, transporting a ram is also easy and may just be as effective for dissemination purposes.

In conclusion, the current study generally provides new insights into the advantages and disadvantages of designed breeding structures, especially the 'interactive cycling' schemes, which is valuable in deciding breeding programmes to adopt for sheep in developing countries in the tropics.

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