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On farm observations to increase genetic gain in breeding schemes for village poultry production – A simulation study

Thinh Tuan Chu[1,2,4], John W.M. Bastiaansen[2], Elise Norberg[1,3] & Peer Berg[1,3]

[1] *Center for Quantitative Genetics and Genomics, Department of Molecular Biology and Genetics, Aarhus University, 8830 Tjele, Denmark*

[2] *Wageningen University & Research Animal Breeding and Genomics, 6709 PG Wageningen, The Netherlands*

[3] *Department of Animal and Aquacultural Sciences, Norwegian University of Life Sciences, 1432 Ås, Norway*

[4] *Corresponding author's email: chu.thinh@mbg.au.dk*

Abstract

To improve genetic gain of breeding programs for village poultry production, breeding schemes with observations obtained in village production systems using individual (VIO) and group recording (VGO) were examined under different levels of genotype-by-environment-interactions (GxE). GxE was modelled by varying the correlation between traits measured in the breeding station and village environments for bodyweight (r_{g_BW}) and egg production (r_{g_EP}). Relative and absolute genetic gains obtained from VIO and VGO were used for comparison between the schemes. Results showed that village observations significantly improved genetic gains compared to the scheme without birds tested in the village. The improvement was only slightly larger with individual observations than with group observations. Higher r_{g_BW} and r_{g_EP} led to lower relative genetic gain, but higher absolute gain of VIO and VGO. It is recommended to apply a breeding scheme using group recording of village performance when strong GxE in breeding for village poultry is expected.

Key words: breeding scheme; GxE; group recording; stochastic simulation; village poultry

Introduction

Introduction of exotic breeds or high yielding hybrids has failed to upgrade the genetic level of the current chicken populations in Ethiopia due to various reasons, such as farmer preference, lack of required input and chicken adaptability (Dana et al., 2010; Wondmeneh et al., 2015). In addition, the application of exotic breeds in an intensive or semi-intensive production system for smallholder villagers brings in lower economic returns than the use of indigenous chicken under a scavenging production system (FAO, 2010; Okeno et al., 2013). Moreover, one of the biggest advantages of indigenous chicken is their disease resistance and adaptability to harsh conditions (Dessie et al., 2000). Therefore, a key approach for delivering a productive and adapted chicken suitable for the production system and acceptable to the farmers, is to improve the indigenous chicken through breeding programs.

A selective breeding program was initiated in 2008 at the Debre Zeit Agricultural Research Centre in Ethiopia (Dana et al., 2011). The ultimate objective of the breeding program is an improved dual-purpose chicken (Horro) for growth and egg production, which also is well-adapted to the semi-scavenging environment of village poultry production. However, the breeding scheme of the program has revealed to be suboptimal as it has shown slow genetic progress and signs of losing adaptability of indigenous chicken after 7 generations of selection (Wondmeneh, 2015). The differences between the conditions at the research station and villages might cause genotype by environment interaction (GxE). At the research station, birds are selected under hygienic conditions, nutritionally adequate diets and well-protected cages, whereas at the villages, birds are subjected to a combination of low food availability, sub-optimal diet, prevalence of diseases and other social interaction factors.

Significant GxE in poultry has been reported in a number of studies (Bekele et al., 2009; Chen et al., 2009; Horst, 1985; Kapell et al., 2012; Mathur & Horst, 1994; N'Dri et al., 2007) and reviews (FAO, 2010; Mathur, 2003). GxE could reduce potential genetic gains of a breeding program. There are, however, only a few studies (Bijma & Arendonk, 1998; Mulder & Bijma, 2005) on design or evaluation of breeding schemes in the presence of GxE, and they are mainly designed for other species than poultry and for commercial production instead of village production. A big challenge for implementing breeding schemes for village poultry is the need for routine collection of observations on individual animals. Group mean of full-sibs and half-sibs can be a possible alternative for village phenotype recording. Studies on pooled data has illustrated that selection based on estimated breeding values (EBV) from pooled observations can be effective, particularly when group members have close relationships (Biscarini et al., 2008; Nurgiartiningsih et al., 2004; Olson et al., 2006; Peeters et al., 2013). However, the use of pooled observations in breeding programs where GxE is present, and where animals with the pooled observations are not candidates of selection, has not been demonstrated.

This paper proposes breeding schemes for village dual-purpose poultry production in the presence of GxE. Stochastic simulation is applied to compare breeding schemes on genetic gain considering group and individual recording and to optimize the data recording effort in villages versus stations. GxE was modelled by varying the correlation between traits measured in station and village environments.

Materials and methods

Breeding schemes

The stochastic simulation program ADAM (Pedersen et al., 2009) was used to simulate 100 replicates for each scenario. The simulation mimicked the situation of the Horro chicken breeding population at the Debre Zeit Agricultural Research Centre, Ethiopia (Dana et al., 2011). The schemes were designed for dual-purpose village poultry production, by including body weight (BW) and egg production (EP) in the breeding goal (Figure 1). The breeding structure consisted of 30 roosters and 300 hens. In each generation, a hen had 4 offspring that were candidates for selection and an additional number of offspring for testing. Sex was randomly assigned to offspring at a 50:50 ratio. The candidates for selection were reared in a research station. Under the station conditions, the birds had phenotypes defined as “station” traits. Birds for testing were transferred to village small holders for recording of phenotypes, which were defined as “village” traits. The village tested birds were not considered as selection candidates, but only gave information for evaluating station selection candidates.

In each generation, selection candidates went through two selection rounds. In the first selection round, 150 of all male candidates were selected after phenotypes for BW were measured both in station and in village. No selection was applied in the females. This round was to ensure a high selection response and to reduce costs of keeping all male candidates until EP was recorded. In the second round, 30 males were selected out of the remaining 150 candidates and 300 females were selected out of all female candidates. Selection round 2 was performed after phenotypes for EP were realized. BLUP selection was applied for both the selection rounds, so information about relatives both in station and in village was used. Selection was simulated for 20 discrete generations.

Trait simulation

Phenotypes of BW and EP were simulated and BW was observed for both male and female birds while EP was observed in females only. In the station environment, BW and EP were denoted as BW_s and EP_s, respectively, whereas in the village environment, the phenotypes were denoted as BW_v and EP_v, respectively. Observations on BW_s and EP_s were realized individually, while BW_v and EP_v were recorded as either group mean or individually. Group records were the average of the simulated phenotypes of 10 paternal-sibs, which were randomly selected from the 40 offspring of a sire. Therefore, members of a group could have both full-sib and half-sib relationship.

The genetic parameters assumed for all traits are shown in Table 1. The parameters of (co)variances, correlation and heritabilities of BW_s and EP_s were based on literature for indigenous chicken in Africa (Dana et al., 2011; Lwelamira et al., 2009; Niknafs et al., 2012; Oleforuh-Okoleh, 2011). We assumed that the village scavenging system would result in a larger environmental variance and a lower heritability compared to the conditions on station. The heritabilities for village traits was set to half the values for the station traits. Additive genetic variances of BW_s and EP_s were assumed equal to those of BW_v and EP_v, respectively. Genetic correlation between BW_s and EP_s was also equal to that of BW_v and EP_v. Genetic correlations between the village and station environments for BW (r_{g_BW}) and EP (r_{g_EP}) were varied to reflect different extent of GxE. To ensure a positive-definite matrix of genetic covariance, the genetic correlation between BW_s and EP_v was approximated by multiplying the average of r_{g_BW} and r_{g_EP} by correlation between BW_s and EP_s (Table 1). This approximation came from assuming that the link between BW_s and EP_v might be through either one of two paths. One path was through correlation between BW_s and EP_s and correlation between EP_s and EP_v, and another path was through correlation between BW_s and BW_v and correlation between BW_v and EP_v. The genetic correlation between BW_v and EP_s was approximated in the same way. Environmental correlation between BW_v and EP_v was assumed to be equal to that between BW_s and EP_s. Other environmental correlations between traits were set to 0 because birds only had records either on the station or in the village environment.

True breeding values of BW_s, EP_s, BW_v and EP_v traits of a bird *i* at generation 0 were scaled to achieve an initial genetic covariance matrix by following equation: $\mathbf{tbv_i} = \mathbf{L'} \times \mathbf{r}$, where $\mathbf{tbv_i}$ is a vector of true breeding values of bird *i*; $\mathbf{L'}$ is the Cholesky decomposition of the initial genetic covariance matrix; and $\mathbf{r}$ is a vector of random numbers from a standardized normal distribution. Means of the traits were 0. Simulation of environmental values of the traits was similar to simulation of true breeding values, with a Cholesky decomposition of the environmental covariance matrix. Phenotypic observation of a trait for an individual was the sum of true breeding value and environmental value. Environmental (co)variances were kept constant through the simulations whereas genetic (co)variance and heritability decreased due to Bulmer effect of selection and inbreeding. True breeding value of the descendants was half of true breeding values of their parents plus Mendelian sampling terms. Mendelian sampling variance of the offspring was determined based on the inbreeding of the parents.

Simulation of group mean observations was done in two steps. The first step was simulation of individual phenotypic observations as described above. The second step was to compute group mean observations. All offspring birds of a sire in a village were randomly assigned into groups of 10 birds. Individual phenotypic observations of those offspring birds were used to calculate group means. Subsequently, the individual phenotypic observations were replaced by group means. For BW_v, 10 paternal-sib of a group had the same group mean observation. For EP_v, phenotypic observations of females of the 10 paternal-sib group were used to calculate the group mean, and phenotypic observations of these females were replaced by the mean.

Simulated scenarios

A reference breeding scheme and 2 alternative breeding schemes were simulated (Table 2). The reference breeding scheme had 1200 candidates for selection and 600, 1200 or 1800 tested birds. Both the selection candidates and tested birds provided information of station phenotypes. For the two alternative schemes, the tested birds did not provide information of station phenotypes but were transferred to village environment to get village phenotypes. In one of the alternatives (breeding scheme VIO), the village birds had individual observations. In the other (breeding scheme VGO), the birds had group mean observation of 10 paternal-sibs. As suggested in Cahaner et al. (1993), Kapell et al. (2012), Mathur and Horst (1994), Mathur (2003) and Chen et al. (2009), a stronger GxE interaction was simulated for EP than for BW, and therefore a lower genetic correlation between station and village measures. The lower correlation for EP than BW came from assumption that traits of reproduction have stronger GxE interaction than traits of production, and traits with lower heritability generally display higher GxE (Mathur, 2003). The values of r_{g_BW} were set at 0.5, 0.7 and 0.9 and r_{g_EP} were 0.1, 0.3 and 0.5.

As a consequence, there were 4 factors investigated: type of breeding schemes, number of tested birds, r_{g_BW} and r_{g_EP}. All three breeding schemes were simulated with all three numbers of tested birds and all 9 combinations of r_{g_BW} and r_{g_EP} resulting in a total of 81 simulated scenarios.

Selection criteria

Breeding was done to optimize production in the village environment and therefore the breeding goal was as follows:

$$H = 0 * BW_s + 0 * EP_s + 0.078 * BW_v + 9.080 * EP_v \qquad (1)$$

An economic value of 0 was assigned to the station traits of BW_s and EP_s with the assumption that only village performance mattered. Economic values given to BW_v and EP_v were from Okeno et al. (2012). Unit of BW was measured in grammes, and EP was cumulative number of eggs produced until 40 weeks of age.

Breeding values were estimated based on data from VIO and VGO using multivariate best linear unbiased prediction (BLUP) models. For individual phenotypic observation, the model was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e} \qquad (2)$$

where $\mathbf{y}$ is a vector of individual phenotypic records of traits of BW_s, EP_s, BW_v and EP_v; $\mathbf{b}$ is a vector of fixed year effects; $\mathbf{a}$ is a vector of animal breeding values of the traits to be estimated assumed $\mathbf{a} \sim MVN[0, \mathbf{A} \otimes \mathbf{G}]$, where MVN is the multivariate normal distribution, $\mathbf{A}$ is the additive genetic relationship matrix among individuals and **G** is the additive genetic (co)variance matrix among the traits as a 4x4 matrix; **X** and **Z** are incidence matrices relating fixed effects and breeding values to phenotypic observations of birds; and **e** is a vector of residuals of the traits assumed $\mathbf{e} \sim MVN\begin{bmatrix} 0 & \mathbf{I_s} \otimes \mathbf{E_s} & 0 \\ 0' & 0 & \mathbf{I_v} \otimes \mathbf{E_v} \end{bmatrix}$, where $\mathbf{I_s}$ and $\mathbf{I_v}$ are identity matrices of station and village observations, respectively, $\mathbf{E_s}$ and $\mathbf{E_v}$ are the environmental covariance matrices (2x2) of the station traits (BW_s and EP_s) and the village traits (BW_v and EP_v), respectively.

For group observations, the same model as (2) was used, except that group averages of the 10 paternal-sibs were treated as if they were individual phenotypic records of each of the ten birds. This is an approximate approach described in Olson et al. (2006).

Selection for the reference breeding scheme was also based on breeding values estimated using model (2), except that the model was a bivariate model applied for 2 traits of BW_s and EP_s only. Selection for the reference scheme was indirect selection, in which selection index was:

$$I = 0.078^{*}\ BW_s + 9.080^{*}\ EP_s \qquad (3)$$

However, (1) was still used as true breeding goal to assess genetic gain of all scenarios.

A combined measure of GxE, which represents the correlation between performances in the two environments, were based on the values of r_{g_BW} and r_{g_EP} with their economic indexes. Genetic correlation between (1) and (3) (r_{g_HI}) was calculated as:

$$r_{g\_HI} = \frac{Cov(H;I)}{\sqrt{Var(H) \times Var(I)}} \qquad (4)$$

Where $Cov(H; I)$ is genetic covariance between H and I; $Var(H)$ is genetic variance of H; $Var(I)$ is genetic variance of I.

Data analysis

For all scenarios, simulated output of total index genetic merit and the inbreeding coefficient from generation 5 to 20 were used for analyses. The index genetic merit of a scenario was the sum of true breeding values indexed with their economic values as in (1). The genetic merit of generation t, G_t, was the average of index true breeding values of all new-born individuals at generation t. Similarly, the inbreeding coefficient at generation t, F_t, was the average of inbreeding coefficients of individuals calculated by pedigree information.

For each replicate, genetic gain per generation (ΔG) was computed as the difference between G_{20} and G_5. The relative genetic gain per generation (*RG*) of VIO and VGO scenarios was calculated as the differences between their genetic gains and the mean of genetic gain of the corresponding reference scenarios divided by the mean of genetic gain of the reference scenarios.

$$RG = \frac{\Delta G_{alternative\ scenario} - Average\ \Delta G_{reference\ scenario}}{Average\ \Delta G_{reference\ scenario}} \times 100\%$$

Where *RG* is relative genetic gain per generation of VIO or VGO scenario over the reference scenario; $\Delta G_{alternative\ scenario}$ is genetic gain per generation of a replicate of VIO or VGO scenario; $Average\ \Delta G_{reference\ scenario}$ is the mean of genetic gain of 100 replicates of the reference scenario corresponding to the VIO or VGO scheme that had the same number of tested animals, and same r_{g_BW} and r_{g_EP}.

Rate of inbreeding per generation were computed as the negative of the slope of the regression of $ln(1-F_t)$ on t for F_5-F_{20} (Nirea et al., 2012).

Summary statistics for *RG* of VIO and VGO scenarios were based on 100 replicates. ANOVA were used to test direct and interaction effects of various factors on *RG*. The differences between scenarios were tested for significance using Tukey's HSD (honest significant difference, $P < 0.05$). Summary statistics for rate of inbreeding of scenarios of VIO, VGO and reference schemes were also computed.

Results

The 4-way interaction of breeding scheme, r_{g_BW}, r_{g_EP} and number of tested animals were significant on *RG* with $p < 0.0001$. As can be seen in Figure 2, all scenarios of VIO and VGO breeding schemes had genetic gain greater than the scenarios of the corresponding reference scheme. Relative genetic gains ranged from 21 to 268%.

The addition of birds tested in the village condition increased *RG.* When number of village tested birds was 600, 1200 and 1800, on average, *RG* was 84, 98 and 112%, respectively.

The VIO breeding scheme had higher *RG* than VGO breeding scheme. On average, *RG* of VIO was 102% while it was 94% for VGO. With 600, 1200 and 1800 tested birds, *RG* of VGO were 81, 94 and 107%, respectively, and *RG* of VIO were 87, 102 and 117%, respectively. In all cases with the same number of village tested birds and the same correlations of r_{g_BW} and r_{g_EP}, *RG* of VGO was lower than that of VIO.

Lower genetic correlations between traits measured on station and village environments, lead to higher *RG.* With the maximum values for r_{g_EP} of 0.5 and r_{g_BW} of 0.9, on average, *RG* was 28% whereas *RG* was 225% for scenarios with the minimum values for r_{g_EP} of 0.1 and r_{g_BW} of 0.5. It seems that the magnitude of increase in *RG* was higher with a reduction in r_{g_EP} than with the reduction in r_{g_BW}. To have a better explanation of the trend of *RG,* r_{g_HI} can be used as an assessment of indirect selection of selection index I to the true breeding goal. *RG* decreased with increasing r_{g_HI} (Table 3).

Genetic gains per generation of VIO and VGO breeding scenarios can be seen in Table 4. Similar to *RG, ΔG* of VIO and VGO scenarios increased with increasing number of village tested animals. Genetic gains of VIO scenarios were also higher than that of VGO scenarios. However, unlike *RG,* lower genetic correlations between traits measured in station and village environments (r_{g_EP} and r_{g_BW}) resulted in lower *ΔG*. Meanwhile, *ΔG* increases with a higher genetic correlation between environments (r_{g_HI}), but at a lower relative increase as can be seen in Table 4.

The rates of inbreeding decreased as number of tested animals increased. They, on average, were 2.00, 1.99 and 1.97% for scenarios with 600, 900 and 1800 tested animals, respectively. Higher rates of inbreeding were found in the VGO scenarios than in the VIO scenarios. The rates of inbreeding, on average, were 1.70% for the reference scenarios, 2.10% for VIO scenarios and 2.15% for VGO scenarios. The rates of inbreeding had a reducing tendency as r_{g_EP} and r_{g_BW} increased.

Discussion

In this study, breeding schemes for village dual-purpose poultry using group and individual recordings of village and station performances at different levels of GxE interaction were compared. Results showed that village observations significantly improved genetic gains of VIO and VGO compared to the reference breeding scheme. The improvement was larger in VIO than in VGO. Increasing number of village tested birds also increased genetic gain. Higher genetic correlations between traits measured in station and village environments lead to lower relative genetic gain, but higher absolute genetic gain.

Effects of village observation on genetic gain

Increasing the number of animals tested in village improved accuracy of selection, and thus genetic gains of VIO and VGO schemes compared to the reference schemes. The main difference between the reference breeding scheme and its alternatives was the type of tested information. Village observations were direct phenotypes while station observations were correlated phenotypes. The reference scheme had only station performance while its alternatives had both station and village performances. Selection in the reference scheme is an indirect selection approach, and therefore, it results in the lowest accuracy of selection compared to its alternatives.

The value of village observations increased when the genetic correlation between station and village traits was lower. The scenarios with r_{g_BW} of 0.9 and r_{g_EP} of 0.5 gave lower relative genetic gain than those with r_{g_BW} of 0.5 and r_{g_EP} of 0.1. Nonetheless, the absolute genetic gain was larger in scenarios with higher genetic correlations as contribution of both station and village observations to accuracy of selection increased.

It has been suggested that if the genetic correlation between performance in the selection and production environments is less than 0.8, breeding program with information from the production environment would be worthwhile to improve genetic gain (Robertson, 1959). Other studies have also shown that a significantly higher genetic gain can be achieved with performance information from the production environment (Bijma & Arendonk, 1998; Mulder & Bijma, 2005). However, when genetic correlation between the performance in selection and production environments is high, for example 0.9, a large number of animals need to be tested in the production environment for a significant improvement in genetic gain.

In our study, relative genetic gains were positive in all scenarios of VIO and VGO with any number of birds tested in village, r_{g_BW} or r_{g_EP}. In other studies, to model GxE, a single trait in two environments is often used (Bijma & Arendonk, 1998; Mulder & Bijma, 2005). To be comparable to other studies, instead of r_{g_BW} and r_{g_EP}, r_{g_HI} should be used as a representative of genetic correlation between station and village environments. It takes into account the variances and covariances of BW and EP traits measured in the two environments with their economic indexes. The value of r_{g_HI} reflects the magnitude of indirect selection on the selection index I to the true breeding goal. It describes the extent of GxE when more than one trait is measured in two environments. In the simulation, r_{g_HI} was 0.16-0.56, which might explain the high relative genetic gains of all VIO and VGO scenarios.

It was expected that both the increases of relative genetic gain and decreases in absolute genetic gain would correspond to increases of r_{g_HI}. However, an increasing tendency of absolute genetic gain did not correspond to the increase of r_{g_HI} (Table 4). Possible explanations may include the two-stage selection for BW in males and that EP is a sex limited trait (50% fewer records for EP than for BW), thus a change of r_{g_EP} has a different impact on absolute genetic gain than a change of r_{g_BW}.

Group versus individual observation

VGO breeding scheme was similar to VIO, except that recordings of village performance were in groups of 10 paternal-sibs. Our findings showed that VGO had lower *RG* than VIO, which is due to a lower accuracy of prediction of breeding values using group recording. Pooling birds in groups reduced the amount of information that was provided for each individual. Nonetheless, VGO had substantially increased genetic gains compared to the reference breeding scheme and reduction of the absolute genetic gain in comparison to the corresponding VIO scenario was at most 6% (Table 4.).

Other studies have analysed pooled data, in which pooled observations were groups of random animals, full-sibs, half-sibs and descendants of maternal grand sire (Biscarini et al., 2008; Nurgiartiningsih et al., 2004; Olson et al., 2006; Peeters et al., 2013). From these studies, it can be concluded that estimation of breeding values from pooled data is theoretically and practically feasible for selection, particularly when the pooled observations are groups of closely related animals.

Biscarini et al. (2008) illustrated that correlations between EBV based on individual observation and the pooled observation of 4 half-sib animals were 0.703-0.748 for EBV of the own animals, 0.814-0.891 for EBV of their sires with more than 10 offspring and 0.847-0.880 for EBV of their dams with more than 4 offspring. Nurgiartiningsih et al. (2004) also demonstrated high correlations between EBV based on individual and group observations which were, on average, 0.844 for EBV of the animals and 0.943 for EBV of their sires. Olson et al. (2006) studied accuracies of predicting breeding values from individual and group observation using simulation. They found that in the absence of pen effects, accuracies of EBV of animals themselves or their sires would be improved when animals allocated in a group were more related and when size of each group was smaller given the same total number of animals.

In our study, to estimate EBV, selection candidates of VGO scenarios could have indirect information from individual observations of the correlated traits (BW_s and EP_s) of their own and parents' performance and direct information from pooled observations of the desired village traits (BW_v and EP_v) of their sibs. The pooled observations were groups of birds that had half-sib and full-sib relationship to the selection candidates. By averaging observations of the sib mixture, effects of dams mated to a sire on their offspring cannot be distinguished. The pooled observations can be only approximated as average of half-sibs. Meanwhile, effects of dams, full-sib and half-sib relationships can be taken into account in predicting EBV of selection candidates in VIO scenarios, which resulted in a higher genetic gain in VIO than in VGO scenarios.

Nonetheless, the differences between accuracy of selection of VIO and VGO were not substantial. With r_{g_BW} of 0.5 and r_{g_EP} of 0.1, accuracy of EBVs of selection candidates was 0.863, 0.892 and 0.917 for VGO with 600, 1200 and 1800 village tested birds, respectively, while the accuracy of EBVs was 0.868, 0.908 and 0.925 for VIO with 600, 1200 and 1800 village tested birds, respectively. With r_{g_BW} of 0.9 and r_{g_EP} of 0.5, the accuracy of EBVs was 0.917, 0.927 and 0.935 for VGO with 600, 1200 and 1800 village tested birds, respectively; and 0.920, 0.934 and 0.940 for VIO with 600, 1200 and 1800 village tested birds, respectively.

Methodology

In our study, high relative genetic gains were achieved for VIO and VGO scenarios, and none of their replicates had negative relative genetic gains. This is due to 3 important assumptions including strong GxE, unchanged number of selection candidates and no common maternal effects.

GxE was modelled for BW at r_{g_BW} of 0.5-0.9 and EP at r_{g_EP} of 0.1-0.5, which represents quite strong interactions. Conventional breeding programs are usually carried out under conditions most favourable for the expression of genotypes. One of the important reasons for this is that GxE is often small, especially for commercial breeds where production animals are reared in enclosed, highly controlled conditions, similar to the station situation. However, the differences between village and breeding station are likely to be more substantial. Therefore, if birds are selected under station conditions of sufficient and balanced diets, absence of infectious diseases and minimum of stress, strong GxE will be expected.

Number of selection candidates was assumed to be unchanged, even for the reference breeding scheme in which tested birds were assumed to have station observations. This assumption is not reasonable in practice, but it was included to quantify benefit of village observations. In theory, as long as genetic correlation between traits measured in station and village environments is less than 1, village observations would provide additional genetic gains for VIO and VGO. Alternatively, if the combined number of birds for selection and village testing was constant, the use of birds for village testing in VIO schemes would not be beneficial for genetic gain with r_{g_HI} above 0.8 due to reduced selection intensity (Chu et al., 2018; Mulder & Bijma, 2005; Robertson, 1959). The use of birds for village testing in VGO schemes would only become beneficial when r_{g_HI} was even lower than the r_{g_HI} of VIO schemes.

Common maternal effects were not included in our simulation. The inclusion of the common maternal effects would have relatively slight effects on genetic gain of VIO if birds from different families are randomly distributed to smallholders. In contrast, it would reduce considerable genetic gains of VGO as members of the group with pooled observations were paternal-sibs. However, the common maternal effects are negligible for the traits of selection in breeding program for village poultry. The traits for selection are often at relatively old age, for example, BW at 16 or 20 weeks of age and EP at 40 or 44 weeks of age. At these ages, common maternal effects for BW and EP would be insignificant. Common maternal effects for BW reduce as birds age (Begli et al., 2016; Dana et al., 2011; Prado-Gonzalez et al., 2003). The dam effects of BW disappeared at 8 weeks of age (Prado-Gonzalez et al., 2003) and 12 weeks of age (Dana et al., 2011). Common dam effects are usually not included in the model for EP traits as they are expressed late in bird life.

Application of breeding schemes for village poultry production

Poultry breeding for village production by poor and nutritionally insecure people in the rural and peri-urban regions of the Sub-Saharan Africa must accept the reality that people prefer dual-purpose chicken in a scavenging or semi-scavenging system (Dana et al., 2010). High investment for commercial housing shed, supplementation of feed and expanded flock size can lead to unsteady net returns. Such a risky investment was one of the main reasons that village farmers were reluctant to spend on the inputs (Wondmeneh, 2015). It is shown that the use of the scavenging production system for smallholders brings in higher economic returns than the use of the semi-intensive or intensive system (FAO, 2010). Therefore, to improve the livelihood of the targeted people, a proper breeding program for village poultry production is required.

Using village observations, breeding schemes VIO and VGO would be appropriate for improving genetic gain of a breeding program and possibly maintaining adaptability traits which are major advantages of indigenous chicken in village production. However, implementation of VIO requires individual records of pedigree and measurement of phenotypes under village conditions. Routine recording phenotypes for individual birds is most likely not possible in village production systems. Measurement of individual phenotypes by smallholder farmers often has low accuracy (Lwelamira, 2012). Implementation of VGO is simpler in practice compared to VIO. Although lower genetic gain is predicted for VGO, the increased accuracy of data recording in VGO may make up for this. Group recording in the VGO breeding scheme reduces the complexity of tracing and recording process. Therefore, the recommended breeding scheme for village poultry production is VGO. Testing 600 birds in the village environment results in significant genetic gain for the program, compared to testing them on station.

Conclusions

Village observations significantly increased genetic gain compared to station observations. The improvement was only slightly larger with individual observations (VIO) than with group observations (VGO). Higher genetic correlations between traits measured in station and village environments led to higher genetic gain, but lower relative genetic gain in VIO and VGO scenarios. In assessing relative genetic gains from village observations for a breeding program in presence of GxE, r_{g_HI}, the genetic correlation between station and village breeding objective, should be used to model GxE as it explained better the magnitude of GxE than r_{g_BW} or r_{g_EP} alone. Breeding schemes that use village group recording are applicable for breeding indigenous dual-purpose poultry where a strong GxE is expected.

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Conflict of interests

The authors declare that they have no conflict of interests.

Authors’ contributions

TTC, EN and PB designed and coordinated the study. TTC, PB and JB designed breeding schemes. TTC and PB conducted all simulations. TTC drafted the manuscript, and all authors read and approved the final manuscript.

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Tables

Table 1: Genetic parameters assumed for simulating body weight (BW) and egg number (EP) in station (s) and village (v) environments: phenotypic variance, heritability (along the diagonal), genetic correlations (above diagonal), and environmental correlations (below diagonal)

	σ_P^2	BW$_s$	EP$_s$	BW$_v$	EP$_v$
BW$_s$	291751	0.41	-0.12	r_{g_BW}	$-0.12\ (r_{g\_BW} + r_{g\_EP})/2$
EP$_s$	130.65	0.02	0.28	$-0.12\ (r_{g\_BW} + r_{g\_EP})/2$	r_{g_EP}
BW$_v$	569610	0	0	0.21	-0.12
EP$_v$	261.29	0	0	0.02	0.14

Note: r_{g_BW} and r_{g_EP}, genetic correlation between traits of station and village environments, are variable factors.

Table 2: Breeding schemes and parameters of genetic correlations between station and village traits

	Alternative breeding scheme

Variables	Reference breeding scheme	Individual observation (VIO)	Group observation (VGO)
Number of tested birds	600, 1200, 1800	600, 1200, 1800	600, 1200, 1800
Type of observations on tested birds	Station	Village	Village
Recording method	Individual	Individual	Group
Genetic correlation between station and village bodyweight (r_{g_BW})	0.5, 0.7, 0.9	0.5, 0.7, 0.9	0.5, 0.7, 0.9
Genetic correlation between station and village egg production (r_{g_EP})	0.1, 0.3, 0.5	0.1, 0.3, 0.5	0.1, 0.3, 0.5

Table 3: Mean of relative genetic gain (*RG* %) of breeding scenarios with different genetic correlations between station and village bodyweight traits (r_{g_BW}) and egg production traits (r_{g_EP}) corresponding to genetic correlations between breeding goal H and index I (r_{g_HI}). S.E.M. was 1%.

r_{g_BW}	r_{g_EP}	r_{g_HI}	Mean of RG
0.5	0.1	0.16	222
0.7	0.1	0.20	170
0.9	0.1	0.23	138
0.5	0.3	0.33	91
0.7	0.3	0.36	78
0.9	0.3	0.40	67
0.5	0.5	0.50	47
0.7	0.5	0.53	37

0.9	0.5	0.56	31

Table 4: Mean of genetic gains per generation (*ΔG*) (± SD) of breeding scenarios with different genetic correlations between station and village bodyweight traits (r_{g_BW}) and egg production traits (r_{g_EP}) using either individual (VIO) or group recording (VGO) of village observations of 600, 1200 and 1800 birds.

r_{g_BW}	r_{g_EP}	r_{g_HI}	600		1200		1800	
			VIO	VGO	VIO	VGO	VIO	VGO
0.5	0.1	0.16	20.4 ± 2.4	20.1 ± 2.7	23.7 ± 2.1	22.2 ± 2.5	25.9 ± 1.8	24.5 ± 2.0
0.7	0.1	0.20	21.9 ± 2.1	21.2 ± 2.2	25.1 ± 2.3	23.7 ± 2.1	26.6 ± 2.0	25.2 ± 2.2
0.9	0.1	0.23	23.7 ± 2.3	23.0 ± 2.1	26.5 ± 2.1	25.3 ± 2.0	28.0 ± 2.0	26.9 ± 2.3
0.5	0.3	0.33	21.1 ± 2.2	20.5 ± 2.2	24.0 ± 2.1	23.4 ± 2.3	25.9 ± 2.2	24.7 ± 2.3
0.7	0.3	0.36	22.8 ± 2.3	21.5 ± 2.3	25.3 ± 2.2	24.6 ± 2.2	27.3 ± 2.1	25.9 ± 2.0
0.9	0.3	0.40	24.7 ± 2.3	24.0 ± 2.3	26.6 ± 2.0	26.2 ± 1.6	28.2 ± 1.8	27.1 ± 1.9
0.5	0.5	0.50	23.0 ± 2.1	22.0 ± 2.4	25.7 ± 2.2	24.7 ± 2.5	27.4 ± 2.1	26.0 ± 2.1
0.7	0.5	0.53	24.0 ± 2.4	23.4 ± 2.3	26.7 ± 2.2	25.7 ± 2.1	28.1 ± 2.5	26.6 ± 2.1
0.9	0.5	0.56	25.8 ± 2.1	25.1 ± 2.2	27.7 ± 2.0	26.5 ± 1.7	28.9 ± 1.9	28.0 ± 2.1

Figure

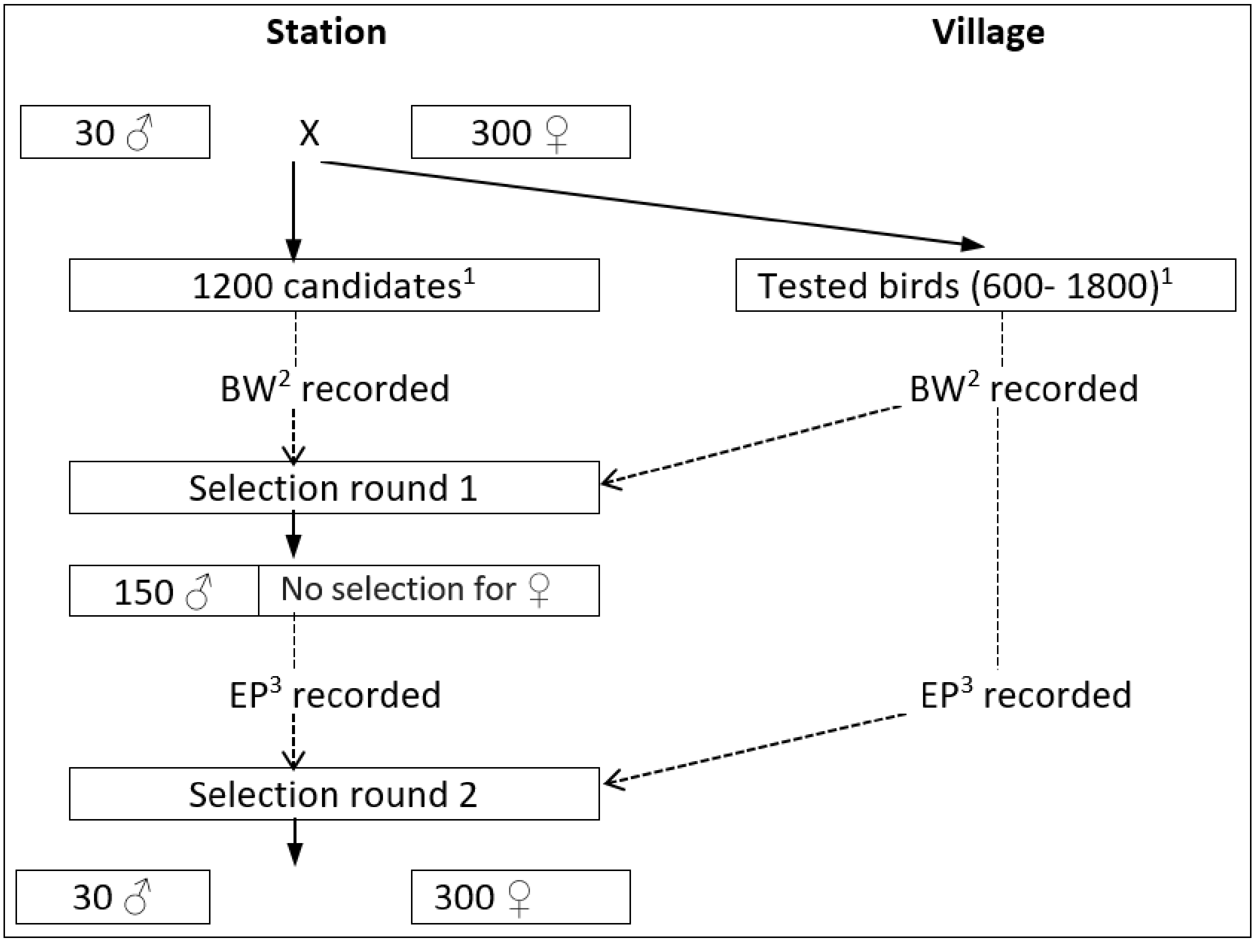

Figure 1: Breeding cycle of a generation. [1] Sex ratio of 1♂:1♀; [2] Bodyweight observed in both ♂ and ♀; [3] Egg production observed in ♀; → Birds reproduced/ selected, --- Observations realized, ⇢ Information for selection

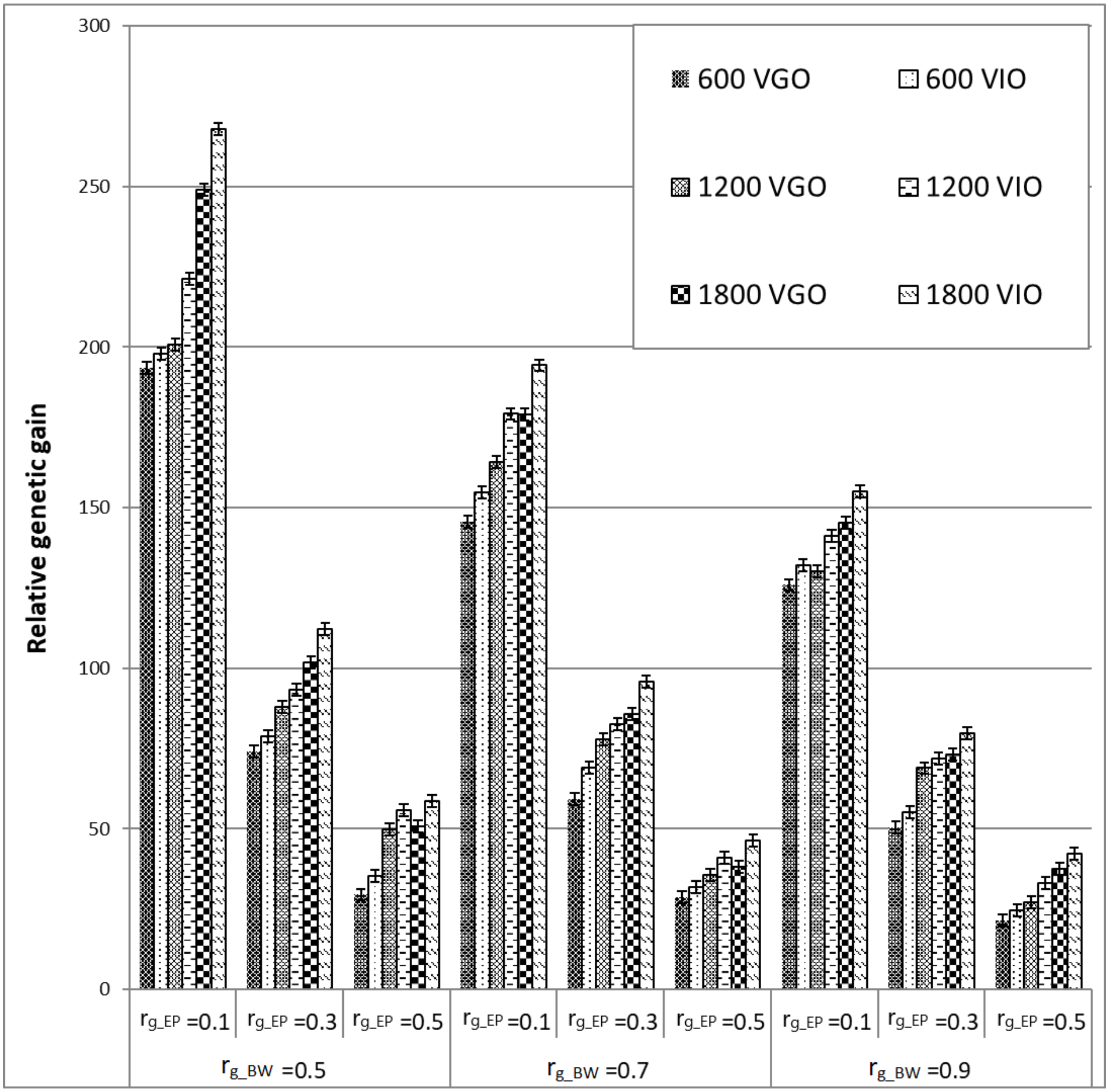

Figure 2: Means of relative genetic gains (%) (± SEM of 2%) of breeding scenarios with different genetic correlations between station and village bodyweight traits (r_{g_BW}) and egg production traits (r_{g_EP}) using either individual (VIO) or group recording (VGO) of 600, 1200 and 1800 village tested birds.