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Converting multi-trait breeding objectives into operative selection indexes to ensure genetic gains in low-input sheep and goat breeding programmes



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ABSTRACT

Small ruminant breeding programmes in low-input production systems are best organised at the community level. Participant farmers have to agree on goal traits and their relative importance. When BLUP breeding values of goal traits are not available in time, appropriate selection indexes can be used to aid visual selection. Taking Ethiopian Abergelle goat and Bonga sheep community-based breeding programmes (CBBPs) as an example, breeding objective functions were defined and selection indexes were constructed and evaluated. Breeding goals for Abergelle goats included early sale weight, survival and milk production. Breeding goals for Bonga included the number of offspring born, sale weight and survival. Economic weights of objective traits can be used in several ways depending on measured traits and the reliability of their genetic parameters. Selection indexes included combinations of objective traits measured on candidates and their dams and situations when Abergelle communities prefer to restrict genetic changes in number of offspring born or adult weight and when Bonga communities prefer to restrict changes in adult weight. Genetic and economic gains were evaluated as well as sensitivity to feed cost assumptions and to repeated dam records. After independent culling on preponderant traits such as coat colour and horn/tail type, sires in Abergelle goat community breeding programmes should be selected on indexes including at least own early live weight and their dams average milk production records. Sires for Bonga sheep programmes should be selected on own early live weight and desirably also on their dam's number of offspring born. Sensitivity to feed cost assumptions was negligible but repeated measurements of dam records improved index accuracies considerably. Restricting genetic changes in number of offspring born or adult weight is not recommended.

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Implications

Breeding objective functions are the basis to construct efficient selection indexes. Representative objective functions, appropriate to Abergelle dual-purpose goats and Bonga meat sheep in community-based breeding programmes, include early live weight and survival in addition to milk yield and reproduction rate, respectively. Selection indexes with different combination of field data sets were evaluated for their accuracy for situations when accurate BLUP breeding values of goal traits are not available in time for selection. The methods used and results obtained can be

readily applied to other tropical goat and sheep breeds, enabling efficient operation of genetic improvement programmes in lowinput livestock systems.

Introduction

About one billion of the world's sheep and goat population is in low income - food deficit countries (FAO, 2018) and most of these animals contribute to livelihoods of smallholder households (Iñiguez, 2011). Multiple efforts are needed to enhance this role of livestock. Genetic improvement organized at community level is a viable and beneficial option (Haile et al., 2019 and 2020; Mueller et al., 2015 and 2019). Design and implementation of genetic improvement programmes require agreement from their

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members on breeding goals and commitment to collect data for selection. Since livestock is the source of a variety of products and services to its holders, livestock breeding goals involve multiple animal traits. In low-input systems, genetic improvement in goal traits must be pursued with low inputs. Some traits may already be near an optimum level and the breeding goal is to attain a desired gain. For example, early growth may be desired but without increasing adult weight or, higher weaning rate is desired but not higher prolificacy. Thus, an agreement is necessary on the choice of traits to be improved by means of selection as well as the relative selection emphasis to be imposed on each trait. There are different methods to identify goal traits and their relative importance in a community herd (Gebre et al., 2012; Mirkena et al., 2012; Mueller et al., 2015; Woldu et al., 2016). Eventually an aggregate breeding objective function with traits of biological and economical interest and their relative importance can be defined for genetic improvement. Once the breeding objective function is agreed on, selection traits need to be identified and measured or scored on selection candidates.

Systematic recording of these measurements or scores, their editing and processing into accurate estimated breeding values (EBVs) and timely availability for selection purposes can be very challenging, particularly in isolated communities where low literacy and limited telecommunication means are an issue. Experience collected in the ongoing small ruminant community-based breeding programmes (CBBPs) recommends the organization of a datamanagement responsibility chain (Haile et al., 2018). Such a chain may start with the employment or empowerment of members of the communities as enumerators with the responsibility of field data recording following a protocolled schedule. The information collected by the enumerators at community level is gathered and subjected to primary editing by local extension officers or regional agriculture-station staff and then submitted to a processing centre where staff with a breeding profile finalize data editing and estimate breeding values with BLUP properties. Editing for data and pedigree consistency often requires backconsultations with regional officers, extension people, enumerators and farmers. Estimated breeding values are eventually returned along the communication chain to the community for selection decisions. Clearly, the data management process, including the maintenance of data bases, needs private and/or public economic and expert support (Haile et al., 2019).

In advanced programmes, EBVs become usually available in time for selection decisions but this may not be feasible, i.e. when the time span between field data recording and selection is very tight and physical access to the sites is difficult due to road conditions or where communities lack electricity supply for wired communication. Hence, a delayed access to updated EBVs can be critical in programmes where surplus progeny is sold early in life or where reproductive activity starts early in life and undesired mating cannot be avoided. These are common situations with the additional problem that usually the heavier animals are sold for cash or are castrated for finishing (Getachew et al., 2010). The most promising candidates are hence prevented to become future breeding animals. Examples for this situation can be found in many programmes where selection is largely based on EBVs estimated for BW at young age, while other traits of interest such as those related with dam's reproduction, survival and milk production are only considered informally during final selection together with appearance traits (Haile et al., 2020).

This data management issue can be addressed in different ways. Cell phone data recording applications including instant consistency checks have been developed and are being tested to speed up the data transfer process. In some instances, data processing steps can be skipped when regional staff have been trained to run BLUP software with total or partial information and therefore provide results in time for selection decisions. Progressive selection has been proposed, for example independent culling in two stages, first on EBVs of traits recorded on dams, such as previous reproduction records or milk records and in a second stage on EBVs of early live weight records (Jembere et al., 2019). If BLUP-EBVs are not available, phenotypic values could be used with a loss of accuracy but without processing delay. In fact, 'dependent' culling levels could be performed if additional early liveweights are available. For example, goat or sheep weaning weights at about 3months of age may be available for selecting a proportion of candidates which allow a desired minimum loss of future benefits or which allow finding a compromise between immediate income from sales and rate of genetic progress (Mueller et al., unpublished).

Selection indexes based on accumulated phenotypic information readily available could be used as provisional or alternative criteria when BLUP-EBVs are not possible to obtain or are not available in time. Knowing the appropriate index trait weights, indexes can be easily calculated as measurements become available on site and selection can be performed immediately. The use of selection indexes would be a simple expedite method for effective selection without delaying farmer's animal sale opportunities, needing only minimal support of extension officers or regional staff. Taking Abergelle goat and Bonga sheep CBBPs in Ethiopia as examples, the aim of our research was to (i) define representative breeding objective functions and (ii) evaluate phenotypic selection indexes with different field data sets including indexes with gain restrictions in some traits. The effect of including or excluding measurements and the sensitivity of genetic and economic gain to parameter assumptions was considered.

Material and methods

Breeding programme models

Abergelle goats and Bonga sheep populations differ markedly in their breeding environments. Abergelle goats, which have a marked breeding season, are common in the northern Amhara region of Ethiopia which is characterized by a long dry season and feed largely on rangeland with limited supplementary feeding. Bonga sheep are not seasonal, are common in the south-western part of Ethiopia, characterized by a long rainy season and mixed perennial crop-livestock production systems. Abergelle goats produce milk for home consumption in addition to selling live animal for meat, and Bonga sheep, a fat-long-tailed breed, is highly valued for its meat production. Households with 5-15 breeding dams in communities of 50-150 households share grazing land and other production resources. The main sources of income from animals in both areas are the sale of surplus offspring and the sale of cull-for-age adults. Labour and feed resources usually limit the number of animals a farmer or community can manage and if this number remains constant over time then farmers may want the animals to breed for an increased number and weight of offspring for sale and, in the case of Abergelle goats, an increased milk production.

The dynamics of a community herd of Abergelle goats or Bonga sheep can be modelled with *nD* breeding dams and biological parameters as follows. Let the mating ratio (dams per sire) be *mr*, then the number of breeding sires *nS* will be nS = nD/mr. The total annual number of offspring born *Ob* may be calculated as the product of *nD*, conception rate (*cr*), reproduction rate (*rr*), the inverse of reproduction interval (*ri*) and prolificacy (*pr*). The number of progeny available for sale or selection will be $Oa = s1 \times Ob$, where *s*1 is the survival rate from birth to the age of sale or selection. Let dams breed for *agD* years and sires for *agS* years with an annual survival rate of *s*² then the number of young females necessary to replace cull-for-age dams can be calculated as the $rF = nD/\sum_{i=1}^{agD} s2^i$ and the number of young males necessary to replace cull-for-age sires as $rM = nS/\sum_{i=1}^{agS} s2^i$. Assuming equal sex ratio, the number of female offspring for sale will be 0.50a - rF and the number of male offspring for sale will be 0.50a - rM. Also, the number of cull-for-age females will be $rF \times s2^{agD}$ and the number of cull-for-age males for sale will be $rM \times s2^{agS}$. The parameterized herd dynamics is illustrated in Fig. 1.

One of each Abergelle goat and Bonga sheep breeding programmes organized at community level were chosen to study breeding objectives and selection criteria. Recent account of the number of total breeding dams and appropriate biological parameters were available from own field data and models of similar programmes studied by Mirkena et al. (2012), Abegaz et al. (2014) and Jembere et al. (2019). These input parameters were used to derive the number of surplus offspring for sale and the number of cull-forage dams and sires (Table 1).

Definition of multi-trait objectives

Considering the community's breeding goal defined arbitrarily as *H*, for *m* breeding objective traits in *H*, we can write the following function $H = f(Y_1, Y_2, \dots, Y_m)$. Since selection produces only slow genetic changes we may use a linear approximation to find changes in *H* due to changes in *Y*, because the mean breeding value for any objective trait will not change greatly in one generation. Then, from a Taylors series expansion of *H* about its value at current means we may write

$$H = \bar{H} + \frac{\delta H}{\delta Y_1} \left(Y_1 - \bar{Y}_1 \right) + \frac{\delta H}{\delta Y_2} \left(Y_2 - \bar{Y}_2 \right) + \dots + \frac{\delta H}{\delta Y_m} \left(Y_m - \bar{Y}_m \right)$$

where $\frac{\delta H}{\delta Y_i}$ is the partial derivative of *H* with respect to Y_i evaluated at $(\bar{Y}_1, \bar{Y}_2, \dots, \bar{Y}_m)$. Less formally, $\frac{\delta H}{\delta Y_i}$ is the rate of change in the average breeding objective for a small change in Y_i when all other traits remain unchanged. It can be estimated numerically by calculating

Table 1

Population and biological input parameter for Abergelle goats and Bonga sheep.

Parameter	Symbol	Abergelle	Bonga
Input parameter			
Number of breeding dams	nD	750	650
Mating ratio (dams per sire)	mr	10	15
Conception rate (dams conceiving per dam exposed)	cr	0.85	0.95
Reproduction rate (dams reproducing per dam conceiving)	rr	0.95	0.95
Reproduction interval (years)	ri	1.00	0.70
Prolificacy (offspring at birth per dam reproducing)	pr	1.05	1.45
Survival between birth and selection (proportion)	s1	0.90	0.95
Annual survival after selection (proportion)	s2	0.95	1.00
Number of breeding dam age groups	agD	5	5
Number of breeding sire age groups	agS	2	2
Mean age of dams and sires at birth of first offspring (years)	afp	1.5	1.5
Average daily milk yield (litres per milking doe)	ADM	0.45	n.a.
Days in milk (days)	DIM	100	n.a.
Derived input parameter			
Number of breeding sires	nS	75	43
Number of offspring born per year	Ob	636	1 215
Number of offspring available for selection	Oa	572	1 154
Number of female offspring for replacement	rF	174	130
Number of male offspring for replacement	rM	40	22
Number of surplus offspring for sale/consumption		357	1 003
Number of cull-for-age dams		135	130
Number of cull-for-age sires		37	22

n.a. = not applicable.

 \overline{H} with current \overline{Y}_i values, then recalculating \overline{H} with a change $\Delta \overline{Y}_i$ in only one trait, to find the change $\Delta \overline{H}$. Then approximately $\frac{\delta H}{\delta Y_i} = \Delta \overline{H} / \Delta \overline{Y}_i$. These marginal changes in \overline{H} per unit changes in goal traits are usually referred to as *economic values* and are denoted

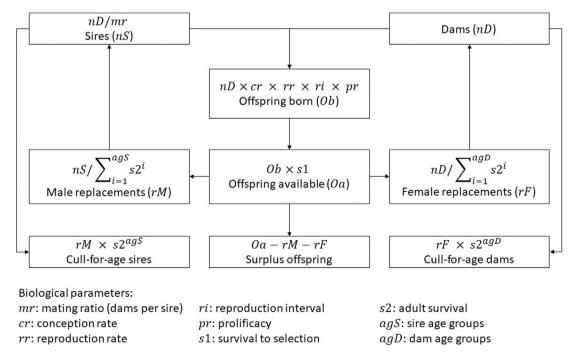


Fig. 1. Constant herd dynamics assuming a known number of breeding dams (nD) and known biological parameters for Abergelle goats and Bonga sheep.

 a_1, a_2, \dots, a_m . Apart from an additive constant we write for aggregate breeding value

$$H=a_1Y_1+a_2Y_2+\cdots+a_mY_m,$$

where the Y_i 's are breeding values for the economically important traits.

Sources of profit and results of preference studies performed in comparable communities with similar animal populations were used to define breeding objective traits. Major sources of profit are the sale of surplus offspring, the sale of cast-for-age animals and in the case of Abergelle goats, the production of milk. The sale of breeding animals or finished animals is assumed to be included in the number of surplus offspring or cast-for age stock. Abergelle milk is not actually sold but it is valued as a cost-saving product. Animal traits affecting these sources of profit targeted for genetic improvement in Abergelle goats are the number of kids reaching sale age (which is also selection age) at about 9-months, the live weight of kids at sale age (SWT), the live weight of cull-for-age dams and cull-for-age sires or adult weight (AWT) and the average daily milk production (ADM). The trait –number of kids reaching sale age- was decomposed into the number of offspring born (**NOB**) and the functional trait survival from birth to sale age (s1). Abergelle communities may want to increase survival and not NOB since this trait implies unwanted increased prolificacy thus, both traits may be targeted with different intentions. Similarly, Abergelle communities may want to increase AWT for additional income from cull-for-age animals or may not want to increase AWT due to management and feeding issues. Thus, AWT was initially considered as a breeding objective trait to test both goal options.

Traits to improve in Bonga sheep are the number of lambs reaching sale age (which is also selection age) at about 6-months, the live weight of lambs at sale age (*SWT*) and the live weight of cull-for-age adults (*AWT*). As in the case of goats, the number of lambs reaching sale age was decomposed into number of offspring born (*NOB*) and survival from birth to sale age (*s*1). As in the Abergelle programme, the weight of cull-for-age adults (*AWT*) was initially included to consider communities interested in increasing live weight of adults or communities interested in restricting changes in adult weight.

Let H_A be the breeding objective function for the Abergelle programme and H_B the breeding objective function for the Bonga programme then

$$\begin{aligned} H_{A} &= a_{NOB} \times BV_{NOB} + a_{s1} \times BV_{s1} + a_{SWT} \times BV_{SWT} + a_{AWT} \times BV_{AWT} \\ &+ a_{ADM} \times BV_{ADM} \end{aligned}$$

$$H_{B} = a_{NOB} \times BV_{NOB} + a_{s1} \times BV_{s1} + a_{SWT} \times BV_{SWT} + a_{AWT} \times BV_{AWT}$$

where the economic values (*a*'s) of traits establish the importance of changes in breeding values (*BV*'s) due to selection. Reduced breeding objective functions were examined for communities which have no interest in improving some traits as mentioned above. Let H_Ar be the reduced Abergelle function H_A but without *NOB* and *AWT* and H_Br be the reduced Bonga function without *AWT*.

Trait weights were calculated using a partial budgeting procedure by which the economic value a_i was calculated as the change in overall profit due to the change in one unit of trait Y_i with the remaining traits maintained at average level. Marginal profit was calculated as the difference between revenue R_i and cost C_i on a dam and year basis. Thus $a_i = f_i \times (R_i - C_i)$ where f_i is the number of expressions of the trait during one year in the herd divided by the number of breeding dams, which is equivalent to the number of expressions per a dam's lifetime. For example, if *n* lambs are sold yearly in a herd with *nD* breeding dams, the number of sale weight expressions per dam per year will be n/nD. Details of the procedures applied and assumptions made for the derivation of the various economic weights in both programmes are in Supplementary Material S1.

Index construction and evaluation

It is assumed that selection of male and female replacements takes place only once at the age of about nine months in the Abergelle programme and at about the age of six months in the Bonga programme, that is before most kids/lambs are presented for sale. At that age, selection candidates will have own BW record (SWT) and may have some or all of the following traits recorded on their dams: number of offspring born (NOB), survival of offspring to sale age (s1), average daily milk yield (ADM, only in the Abergelle programme) and adult weight (AWT). Daily milk yield in Abergelle goats refers to milk available for human consumption assuming a negligible effect of prolificacy on ADM. The average daily milk yield of a dam in a lactation period can be programmed by means of the 'test interval method' (ICAR, 2020). The method adds the products of average milk yields between successive test days and number of days between test days to calculate the lactation yield which is divided by the total days in milk (DIM) gives ADM. The dam's adult weight record was arbitrarily defined as the postpartum weight and for simplicity, assumed to be directly correlated to the dam's cull-for-age weight and the sire's cull-for-age weight. Traits measured on dams may be based on one or on *n* repeated records, each record corrected for the current herd average. The corrected record

of trait *X* can be obtained as $X = \sum_{i=1}^{n} (X_i - \overline{X}_i)/n$, the average deviation from the mean. This is a convenient approximation easily programmed on a spreadsheet in a local computer or cell phone when unbiased corrections from mixed model analyses are not available. When animals with different sets of data are compared, indexes must be calculated using deviations from means rather than actual values. However, if all animals have equal information actual values may be used.

The following selection traits were considered: *SWT*, ds1, d*ADM*, d*NOB* and d*AWT*, where the 'd' indicates the trait is measured on the dam of the selection candidate and allowance was made for the genetic relation (0.5) between the dam and the selection candidate. Three selection indexes were analysed for each breed. Index1A for Abergelle and Index1B for Bonga, respectively, are indexes based solely on *SWT*, equivalent to single trait selection. A second index includes main traits for each breed, for Abergelle Index2A = *SWT* + ds1 + d*ADM* and for Bonga Index2B = *SWT* + ds1 + d*NOB*. The third index includes all traits, for Abergelle Index3A = *SWT* + ds1 + d*ADM* + d*NOB* + d*AWT* and for Bonga Index3B = *SWT* + ds1 + d*ADM* + d*AWT*.

From standard selection index theory (Hazel, 1943) we know that with *n* traits in index *I* and *m* traits in breeding objective *H* and with phenotypic covariance's among index traits **P** and genetic covariance's among index and objective traits **G** it can be shown that Pb = Ga with solutions $b = P^{-1}Ga$, the index trait weights. Several indexes were constructed in this way and evaluated in terms of the genetic gains obtained and in terms of the importance of traits included in the index. The importance of a trait in a selection index was evaluated by assessing the effect of dropping the trait from the index. Let I^* be the index obtained when the *k*-th trait is omitted from the full index I. Then the efficiency of the reduced index relative to the full index is $\sqrt{1 - b_k^2 / R_{kk} \sigma_l^2}$, where b_k is the index weight of trait k and R_{kk} is the inverse element in P^{-1} . This result makes it relatively easy to assess whether dropping any trait from the index will seriously affect response to selection. The value of the trait in the index or percent reduction in genetic gain for aggregate genotype if the trait is omitted is then

$1-\sqrt{1-b_k^2/\boldsymbol{R}_{kk}\sigma_l^2}.$

Selection indexes were derived with *P* and *G* calculated from parameters in Table 2. These parameters are largely based on the weighted averages published by Jembere et al. (2017) for goats and Safari et al. (2005) for sheep, rounded towards parameters from tropical and Ethiopian breeds and considering additional recent estimates. There were only small differences between goats and sheep in reproduction, survival and early live weight estimates so that the same heritabilities, phenotypic and genetic correlations were used for Abergelle and Bonga populations although covariances were derived using phenotypic variances for each population. Phenotypic variances were calculated from own data, considering rounded coefficients of variation and actual means obtained in the field. A convenient Fortran code was written to perform the various calculations including the selection index software SELIND (Cunningham and Mahon, 1977) as a core subroutine.

Selection indexes which restrict gains were constructed with Cunningham's et al. (1970) method based on augmenting the basic unrestricted equations Pb = Ga by adding a dummy variable to the index, a row and column to P and a row of zeros to G. The resulting equations are

$$\begin{bmatrix} P & G_i \\ G'_i & 0 \end{bmatrix} \begin{bmatrix} b \\ b_{dummy} \end{bmatrix} = \begin{bmatrix} G \\ 0 \end{bmatrix} a \text{ or } P^*b^* = G^*a$$

The (n + 1)-th column of P^* consists of the *j*-th column of *G* for its first *n* elements, with a zero in the final position. This last trait is then the trait restricted to no genetic change. The restricted index weightings are found as usual $b^* = P^{*-1}G^*a$. The method can be extended to restrict more traits by adding corresponding rows and columns. This method was used to find indexes which restrict gains in *NOB* and *AWT* for interested Abergelle communities and to restrict gains in *AWT* for interested Bonga communities.

Response to selection

With average selection intensity *i* and generation length *L* (in years), the annual response to selection in trait 1 when selecting for the same trait 1 can be written as $R_{1.1} = h_1^2 \sigma_{P1} i/L$ where h_1^2 is the heritability and σ_{P1} the phenotypic SD of trait 1 (Falconer, 1981). Response to selection in trait 2 when selecting for trait 1 can be written as $R_{2.1} = r_G h_1 h_2 \sigma_{P2} i/L$, where r_G is the genetic correlation between trait 1 and trait 2. With index selection, annual response to selection in *H* is $R_{H,I} = \sigma_I b_{HI} i/L = r_{IH} \sigma_H i/L$. Response in trait Y_j is the regression of the trait on index times SD of index or $\frac{\cos(Y_j,I)}{\sigma_i^2} \times \sigma_I$, where $\cos v(Y_j,I) = b_1 G_{1j} + b_2 G_{2j} + \cdots + b_n G_{nj}$, where the *b*'s are index weights and the *G*'s are genetic covariances and

where the variance of the index is $\sigma_l^2 = \mathbf{b}' \mathbf{P} \mathbf{b}$. In this way changes in mean breeding value due to index selection are calculated for all *m* goal traits. The contribution of change in the *j*-th trait to economic gain is $a_j \times \frac{cov(Y_{j,l})}{\sigma_l}$ and the sum of these contributions is σ_l , the value in economic units of the change in aggregate genotype achieved in one generation by one SD of selection on the index. For generality, genetic and economic gains were presented in these units. Annual genetic and economic gains with average (over sexes) selection intensity *i* were obtained by simply multiplying with *i*/*L*, where selection intensities were calculated from proportions selected and generation lengths calculated from breeding dam and sire age structures derived from input data in Table 1.

Sensitivity to input parameter sampling

The reduced breeding objective functions (those without *NOB* and *AWT*) were used to test sensitivity to variations in assumed prices and costs. The similarity of breeding objectives with the same traits but different economic weights was determined through its genetic correlation. Suppose H_1 is the reference breeding objective and H_2 is the alternative tested with vectors of economic weights \mathbf{a}_1 and \mathbf{a}_2 , then their genetic correlation is $r_{H_1H_2} = \mathbf{a}_1'\mathbf{Q}\mathbf{a}_2/\sqrt{(\mathbf{a}_1'\mathbf{Q}\mathbf{a}_1)(\mathbf{a}_2'\mathbf{Q}\mathbf{a}_2)}$, where $\mathbf{a}_1'\mathbf{Q}\mathbf{a}_2$ is the covariance of objective functions, $\mathbf{a}_i'\mathbf{Q}\mathbf{a}_i$ is the variance of H_i (σ_{Hi}^2) and \mathbf{Q} is the covariance of traits in H (James, 1982).

The sensitivity of genetic and economic gain to some assumed parameters was studied considering the following cases. Feed costs can be very variable depending on the particular community assets, environment, reproduction pattern of the herd, access to alternative feed sources, etc. For example, feed costs may be very low if crop residues are regularly available in quantity and quality or range pasture is not limiting nutrition needs. Contrariwise, feed costs may be high if it needs to be transported from far or when it is scarce. Sensitivity of results when eliminating all feed costs or when doubling all feed costs was tested for the reduced breeding objectives.

The effect of the accuracy of dam records on genetic and economic gain was studied when repeated measurements are available. Repeated measurements decrease permanent environmental effects and therefore decrease phenotypic variance. For example if phenotypic variance is σ_P^2 then the phenotypic variance of the mean of n repeated measurements is $\sigma_P^2(1 + (n - 1)t)/n$, where t is the repeatability of the trait measured. The response to selection with n repeated records is $\sqrt{n/(1 + (n - 1)t)}$ times as much as if selection were made on only one record per animal. The effect of three measurements instead of only one measurement of all traits measured on dams was evalu-

Table 2

Abergelle goats and Bonga sheep trait means, CV, repeatabilities and genetic and phenotypic parameter matrix.

Traits	Abergelle		Bonga		Repeatability ¹	Parameter matrix ²					
	Mean	CV	Mean	CV		NOB	s1	SWT	ADM	AWT	
Number of offspring born (NOB, No.)	0.85	0.50	1.87	0.30	0.15	0.05	0	-0.10	0.25	0	
Survival from birth to sale age (s1, proportion)	0.90	0.40	0.95	0.40	0.10	0	0.08	0.10	0.12	0	
Offspring sale weight (SWT, kg)	18.0	0.14	22.0	0.14	n.a.	-0.10	0.30	0.28	0.10	0.70	
Average daily milk yield (ADM, litre)	0.45	0.40	n.a.	n.a.	0.50	0.08	0.50	0.20	0.32	0	
Adult sale weight ³ (AWT, kg)	25.0	0.15	42.0	0.11	n.a.	0	0	0.68	0	0.35	

Derived from Jembere et al. (2017), Safari et al. (2005), Aljumaah (2019), Getachew et al. (2020) and own field data.

n.a. = not applicable.

¹ Repeatabilities of *NOB* and *s*1 for both breeds, repeatability of *ADM* for Abergelle goats.

² Heritabilities along diagonal, phenotypic correlations above diagonal and genetic correlations below diagonal.

³ Adult sale weight refers to mean weights of cull-for-age females; mean AWT of cull-for-age males is 32.0 kg and 55.0 kg for Abergelle goats and Bonga sheep, respectively.

ated for the reduced breeding objective assuming repeatabilities of Table 2.

Results

Breeding objective functions

Economic weights of goal traits were obtained following procedures detailed in Supplementary Material S1. Resulting breeding objective functions for each programme including all traits or reduced functions including only main traits and functions with different feedcost assumptions are in Table 3. Variances of breeding objective functions (σ_H^2) for Bonga programmes are much higher than variances for Abergelle programmes due to higher economic values in meat related traits not compensated by the additional milk production trait in Abergelle functions. Bonga breed has a much higher prolificacy and shorter reproduction interval than Abergelle leading to high economic income and trait importance.

Defining H_Az as the objective function when Abergelle communities set zero economic value to changes in *NOB* and *AWT* ($a_{NOB} = 0$ and $a_{AWT} = 0$); and defining H_Bz as the function when Bonga communities set zero economic value to changes in *AWT* ($a_{AWT} = 0$). Then the correlation of H_A with H_Az resulted 96.6% and the correlation of H_B with H_Bz resulted 99.6%. The high correlations suggest that breeding objective functions with no economic value for these traits would still adequately represent the aggregate breeding goals in both populations.

Reduced breeding objectives H_Ar and H_Br with main traits in each case had only slightly smaller variances than H_A and H_B and, as expected, intermediate variances of breeding objective functions with low and high feed cost. Correlations between reduced objectives resulted all very high suggesting a negligible effect of assumptions on feed cost in the range tested (zero costs – double costs). This might be explained by the low feed costs relative to product prices assumed in both programmes.

Predicted genetic and economic gains

Expected genetic and economic gains in Abergelle goal traits (in H_A) when selecting for different selection indexes are in Table 4. Selecting for high Index1A, which is equivalent to single trait selection for *SWT*, improves all positively correlated traits. The negative sign for genetic gain in *NOB* is due to the negative genetic correlation between *SWT* and *NOB* (-0.1), not compensated with a sufficiently high economic value (a_{NOB}). Selecting for Index2A, including ds1 and dADM, total economic gain increases 43% (from \$1.94 to \$2.77) and selecting for Index3A, including also dNOB and dAWT, total economic gain increases very little more. Selecting for an index which restricts these traits to zero genetic gain reduces economic gain from \$2.81 to \$2.30.

In the Bonga programme, using Index2B instead of selecting only on *SWT* (Index1B) increases total economic gain 9% (from \$3.66 to \$3.98) mainly due to contributions from genetic changes in *NOB*. Using Index3B (including *AWT*) adds very little to economic gain (Table 5). Restricting genetic changes of *AWT* to zero reduces economic gain to about half (\$1.86). In general, if farmers want to restrict *NOB* and/or *AWT* to zero genetic change then selection has to be based on indexes including these traits (d*NOB* and/or d*AWT*) otherwise it may be impossible to achieve the restrictions or the result may become extremely uneconomic. Clearly, restricting genetic gains in these traits is rarely justifiable in both Abergelle

Table 3

Economic values of breeding objective traits in US Dollar and variance (σ_{H}^{2}) of different breeding objective functions for Abergelle goats and Bonga sheep.

			Breeding of					
Breed	Breeding objective description	Symbol	NOB	s1	SWT	ADM	AWT	σ_{H}^{2}
Abergelle	All traits	H _A	\$18.58	\$18.82	\$1.04	\$57.33	\$0.48	62.82
Abergelle	Reduced to main traits	H _A r	n.a.	\$18.82	\$1.04	\$57.33	n.a.	55.21
Abergelle	Main traits, low feed cost	H _A rf	n.a.	\$19.06	\$1.06	\$57.33	n.a.	55.64
Abergelle	Main traits, high feed cost	H _A rF	n.a.	\$18.58	\$1.02	\$57.33	n.a.	54.79
Bonga	All traits	H_B	\$64.58	\$65.35	\$2.95	n.a.	\$0.45	160.00
Bonga	Reduced to main traits	$H_B r$	\$64.58	\$65.35	\$2.95	n.a.	n.a.	150.44
Bonga	Main traits, low feed cost	H _B rf	\$66.12	\$66.12	\$3.01	n.a.	n.a.	156.03
Bonga	Main traits, high feed cost	H _B rF	\$63.03	\$64.58	\$2.90	n.a.	n.a.	145.14

NOB = number of offspring born, s1 = survival to sale age, SWT = sale weight, ADM = average daily milk yield, AWT = adult weight, n.a. not applicable.

Table 4

Genetic and economic gains following selection on different indexes for Abergelle goats breeding objective (*H_A*). Genetic gains per generation achieved by one SD of selection on index. Economic gains in US Dollar.

	No restricted	NOB and AWT restricted						
	Index1A ¹		Index2A ²		Index3A ³		Index3A	
Item	Genetic gain	Economic gain	Genetic gain	Economic gain	Genetic gain	Economic gain	Genetic gain	Economic gain
Trait in breeding objective								
Number of offspring born (NOB)	-0.005	-\$0.09	-0.002	-\$0.03	-0.003	-\$0.05	0.000	\$0.00
Survival to sale age (s1)	0.016	\$0.30	0.022	\$0.42	0.024	\$0.45	0.021	\$0.39
Sale weight (SWT)	0.706	\$0.73	0.557	\$0.58	0.538	\$0.56	0.175	\$0.18
Average daily milk yield (ADM)	0.011	\$0.61	0.027	\$1.57	0.028	\$1.62	0.030	\$1.73
Adult weight (AWT)	0.798	\$0.38	0.495	\$0.24	0.467	\$0.22	0.000	\$0.00
Total		\$1.94		\$2.77		\$2.81		\$2.30
Index accuracy (r_{HI})	0.245		0.349		0.354		0.290	

¹ Index1A based on SWT.

² Index2A based on SWT, dams s1 and dams ADM.

³ Index3A based on dams NOB, SWT, dams s1, dams ADM and dams AWT.

Table 5

Genetic and economic gains following selection on different indexes for Bonga sheep breeding objective (H_B) . Genetic gains per generation achieved by one SD of selection on index. Economic gains in US Dollar.

	No restricted	AWT restricted							
	Index1B ¹		Index2B ²		Index3B ³		Index3B		
Item	Genetic gain	Economic gain	Genetic gain	Economic gain	Genetic gain	Economic gain	Genetic gain	Economic gain	
Trait in breeding objective									
Number of offspring born (NOB)	-0.007	-\$0.43	-0.002	-\$0.13	-0.002	-\$0.16	0.003	\$0.19	
Survival to sale age (s1)	0.017	\$1.10	0.020	\$1.28	0.021	\$1.39	0.020	\$1.33	
Sale weight (SWT)	0.862	\$2.54	0.822	\$2.42	0.810	\$2.39	0.116	\$0.34	
Adult weight (AWT)	0.984	\$0.44	0.909	\$0.41	0.889	\$0.40	0.000	\$0.00	
Total economic gain		\$3.66		\$3.98		\$4.02		\$1.86	
Index accuracy (r_{HI})	0.290		0.315		0.317		0.152		

¹ Index1B based on SWT.

² Index2B based on SWT, dams s1 and dams NOB.

³ Index3B based on dams NOB, SWT, dams s1 and dams AWT.

Table 6

Genetic and economic gains following selection on different indexes for Abergelle goats reduced breeding objective ($H_A r$) and sensitivity to feed cost assumptions and increased dam information accuracy. Genetic gains per generation achieved by one SD of selection on index. Economic gains in US Dollar.

	Index1A ¹		Index2A ²		No feed costs Index2A		Double feed costs Index2A		Repeated dam records Index2A	
Item	Genetic gain	Economic gain	Genetic gain	Economic gain	Genetic gain	Economic gain	Genetic gain	Economic gain	Genetic gain	Economic gain
Trait in breeding objective										
Survival to sale age (s1)	0.016	\$0.30	0.020	\$0.38	0.020	\$0.39	0.020	\$0.38	0.025	\$0.47
Sale weight (SWT)	0.706	\$0.73	0.301	\$0.31	0.303	\$0.32	0.298	\$0.30	0.267	\$0.28
Average daily milk yield (ADM)	0.011	\$0.62	0.056	\$3.22	0.056	\$3.21	0.056	\$3.21	0.071	\$4.06
Total economic gain		\$1.65		\$3.92		\$3.92		\$3.89		\$4.80
Index accuracy (r_{HI})	0.222		0.525		0.525		0.526		0.647	

¹ Index1A based on SWT.

² Index2A based on SWT, dams s1 and dams ADM.

Table 7

Genetic and economic gains following selection on different indexes for Bonga sheep reduced breeding objective (H_Br) and sensitivity to feed cost assumptions and increased dam information accuracy. Genetic gains per generation achieved by one SD of selection on index. Economic gains in US Dollar.

Index1B ¹		Index1B ¹ Inc		Index2B ²		No feed costs Index2B		Double feed costs Index2B		dam records
Item	Genetic gain	Economic gain	Genetic gain	Economic gain	Genetic gain	Economic gain	Genetic gain	Economic gain	Genetic gain	Economic gain
Trait in breeding objective										
Number of offspring born (NOB)	-0.007	-\$0.44	-0.001	-\$0.09	-0.001	-\$0.10	-0.002	-\$0.11	0.002	\$0.16
Survival to sale age (s1)	0.017	\$1.12	0.020	\$1.31	0.020	\$1.33	0.020	\$1.28	0.025	\$1.64
Sale weight (SWT)	0.862	\$2.54	0.808	\$2.38	0.808	\$2.43	0.808	\$2.34	0.767	\$2.26
Total economic gain		\$3.22		\$3.60		\$3.66		\$3.51		\$4.05
Index accuracy (r_{HI})	0.263		0.292		0.292		0.293		0.332	

¹ Index1B based on SWT.

² Index2B based on SWT, dams s1 and dams NOB.

and Bonga programmes unless their economic values are highly negative.

Tables 6 and 7 show gains in reduced breeding objectives $H_A r$ and $H_B r$ when selecting for Index1 and Index2. As expected, Abergelle programmes benefit greatly from using Index2A which includes dams milk performance information (r_{HI} increases from 0.222 to 0.525), less so Bonga programmes where index2B adds little to index accuracy (r_{HI} increases from 0.263 to 0.292). An interesting result is the much higher total economic gain when selecting on high Index2A for $H_A r$ than when selecting on high Index2A for H_A . Thus, using indexes constructed with the same traits to improve breeding

objective functions with the same economic values for the common goal traits gave different results. The reason lays in the correlated responses in traits of H_A which are not considered in H_Ar . This highlights the importance of including in the breeding objective function all traits affecting profit. In this example, H_A , H_Az and H_Ar give different results with the same selection information available. This is also important when comparing the present results with previous studies (Abegaz et al., 2014; Mirkena et al., 2012; Jembere et al., 2019) where breeding objective functions correspond to our reduced objectives, implicitly ignoring desired or undesired correlated responses in *NOB* and *AWT*.

Sensitivity to parameters

The effect of eliminating all feed costs or doubling all feed costs was tested with the reduced breeding objectives of both programmes. No important effect was observed in either programme (Tables 6 and 7). The result was expected as feed costs were relatively low compared to prices. In particular, the Abergelle programme did not consider feed costs for increased milk production. Heritabilities of NOB, s1 and ADM in Table 2 were assumed to be based on one record. With more records, accuracies increase and genetic gains increase. In the case of Abergelle, response in the reduced breeding objective and selecting for Index2A with three measurements on dams for s1 and ADM instead of only one measurement, economic gain increased from \$3.92 to \$4.80, largely due to higher genetic gain in ADM (Table 6). Similarly for Bonga selected for Index2B the economic gain in $H_{\rm B}r$ increased from \$3.60 to \$4.05 due to increases in genetic gains of both s1 and NOB (Table 7).

Discussion

Breeding objectives and selection indexes

The choice of breeding goal traits for the two programmes was based on regular herd products and published farmer preference studies. The breeding goal traits chosen for the Abergelle programme coincided with those of Abegaz et al. (2014) and Jembere et al. (2019) with the exception that in the present study AWT and NOB were included to study the effect of either calculating an economic value or restricting gains in these traits. Both situations may occur depending on the region and production system. Combining revealed and stated farmer preferences of Abergelle farmers, Woldu et al. (2016) derived live weight as being the most important goal, second in importance resulted disease resistance and third was male candidate's libido. They concluded that milk production should be included if recording is feasible. The breeding goal traits chosen for the Bonga programme coincide broadly with Mirkena et al. (2012) who considered goal traits based on the result of farmer preference studies. Mirkena et al. (2012) considered twinning rate, survival to weaning and yearling BW. The present study considered NOB which includes twinning rate (prolificacy), s1 which extends survival to sale age and SWT which is live weight somewhat earlier than yearling weight. In the present study we included adult weight for Bonga programmes to test farmers' interest in additional income from cull-for-age live weights or interest in maintaining AWT with no genetic gain.

In any case, the breeding goals chosen are probably incomplete for particular communities or individual farmers. There may be interest to consider additional animal products such as manure and skins or specific preferences related to adaptation, functional and appearance traits. Adaptation traits, such as those related to disease resistance, ability to access and digest rough forage, ability to avert predators, resistance to heat or cold, compensatory growth, etc. can be very important, particularly in low-input systems where sanitary conditions are poor, parasite and disease incidence is high, access to animal healthcare is limited, shelter from heat and cold is unavailable, etc. Survival is seen as the underlying component trait for adaptation and in the case of CBBPs favourable adaptation genes and other breeding objective preferences of base farmers are secured in the sires as these are born from what farmers considered as 'best' (=adapted) females (Mueller et al., 2015). We found a rather small effect of survival, similar to Kosgey et al. (2003), related to its low heritability.

Some appearance and functional traits like coat colour, horn type, easy care, docility, etc. can be valued and can be considered objectively. For example, Gizaw et al. (2010) included appearance and adaptation trait in the breeding objective of Menz sheep, represented by chest girth and faecal worm egg count, respectively. While complete objective functions are desirable it has also been shown that participatory and bio-economic approaches are often matching or complementary. According to Gizaw et al. (2018), participatory approaches and bio-economic approaches have both drawbacks and are complementary rather than opposed, taking account of farmer's indigenous knowledge and choices and genetic properties and accurate economic values.

Economic values can be calculated in detail. For example, not all traits of the breeding objective are expressed with the same frequency nor at the same time. Ponzoni (1986) proposed two approaches to deal with this fact: 1. Calculating all incomes and expenses in one year (which accounts for frequency but not time lag) or 2. Using the discounted gene flow (which accounts for both, frequency and time lag). The latter method increases the importance of traits expressed early in life (e. g. *SWT*), whereas the opposite is true for traits expressed late in life (e. g. *ADM* and *AWT*). We used the first approach assuming compensation in the case of Abergelle and small effect in the case of Bonga. Unless discount rates are very high, this assumption is considered negligible.

While it is recommended to include feed intake as a goal trait (James, 1986), we used the approach of subtracting marginal feed costs from product price and estimating marginal feed costs as related to food maintenance requirements proportional to metabolic weight, following procedures described by Ponzoni (1979). Feed intake calculated from animal energy requirements related to live weights, physiological status and voluntary activity were used by Kosgey et al. (2003) and other authors. But feed costs may be ignored altogether when kidding/lambing or fattening coincides with periods of surplus range pasture production as in Bonga. We tested the sensitivity of breeding programmes when feed costs are twice as high as average and found only small effects on economic gain. Certainly, feed cost may reach even higher values, for example in situations of natural feed scarcity due to prolonged, acute drought. However, under such extreme scenarios of feed scarcity, the survival of the animals is threatened and the existence of any breeding programme becomes questionable. The results reported are a relief since feed cost assumption affect various traits. This result also prevented us from further attempts of detailed calculation of economic values for example feed transport costs and extra labour due to feeding costs.

Genetic gains in Tables 4-7 were all given per generation and when selecting with an intensity of one SD of the respective index. Annual genetic gains, with selection intensity *i*, are obtained by multiplying those gains with i/L. Selection intensity i can be obtained as s(p) the standardised selection differential achieved by selecting the best fraction p of a normal distribution. For the Abergelle programme, for example, selection intensity of females and males is s(174/286) = 0.63 and s(40/286) = 1.58, respectively and the average age of females and males is 3.40 and 1.99 years, respectively (Table 1) which makes i/L = 0.41 or i/L = 0.29 with no selection pressure on female candidates, a more common situation. For Bonga these two figures are 0.64 and 0.40, respectively. Due to its higher reproduction and consequent higher number of selection candidates, selection intensity is potentially much higher in Bonga than in Abergelle programmes. For example, selecting only males for Index2 to improve reduced aggregate genotypes in the Abergelle programme gives annual genetic gains in survival rate of $0.020 \times 0.29 = 0.006$, in kid sale weight of 0.301 kg \times 0.29 = 0.087 kg and in average daily milk yield of $0.056 \ l \times 0.29 = 0.016 \ l$. Total annual economic gain per doe is $3.92 \times 0.29 = 1.14$ and multiplied by 750 breeding does gives \$852.60 per year to the Abergelle community (Table 6). It should

be noted here that these results apply with various input parameters and assumptions. It is advisable to recalculate results as more accurate genetic and economic parameters become available. Both breeding objectives and selection indexes can be updated as new information becomes available.

Implications for breeding programme design and operation

The derived economic values (a's) of objective traits can be used in several ways. When BLUP EBV's of breeding objective traits are available, selection can be performed on aggregate breeding values calculated as $\sum_{i=1}^{m} a_i \times EBV_i$. In this case, BLUP EBV's should be derived from a complete multivariate analysis accounting for covariance of traits in the breeding objective (Mrode, 2005, page 20). As we have seen, when BLUP EBV's are not available, for whatever reason, economic values can be used to calculate standard indexes with measurements X_i as $\sum_{i=1}^n b_i \times X_i$ with $\boldsymbol{b} = \boldsymbol{P}^{-1}\boldsymbol{G}\boldsymbol{a}$. If the *a*'s need to be changed frequently it is useful to calculate BLP (Best Linear Prediction) *EBV*'s. The columns of $P^{-1}G$ are the subindexes to predict BLP EBV's of traits in the objective so that we can select on $\sum_{i=1}^{m} a_i \times EBV_i$, where the *EBV*'s have BLP properties. When some of the traits have unreliable **P** and **G** parameters a reduced index can be constructed leaving those traits with little contribution to the index variance out (Williams, 1962). If only heritabilities are known with sufficient reliability a heritability index $\sum_{i=1}^{n} h_i^2 \times a_i \times X_i$ can be used (Heidhues and Henderson, 2010). If all parameters are completely unreliable but all traits of the breeding objective (Y's) are measured, a base index (Williams, 1962) may be used. Base indexes are calculated as the sum of *a*-weighted phenotypic values, $\sum_{i=1}^{m} a_i \times Y_i$. In practice there will be selection candidates with partial or

In practice there will be selection candidates with partial or missing data. If there are many such animals, appropriate indexes should be constructed with the information available. If there are only a few animals with missing data, the contemporary group mean can be assigned as their expected value. More conveniently, all measurements can be recorded as deviations from the mean in which case missing values will be zero. It may also be convenient to adjust the measurements to means and variances actually used in the derivation of the particular index. For example, field measurement *X* with mean \overline{X} and SD σ_X can be standardized to the population mean μ and population SD σ used to obtain index weights as $(X - \overline{X})/\sigma_X \times \sigma + \mu$.

In all these alternatives to the standard index a basic condition is that selection must be performed within the contemporary group. We cannot compare BLP EBV's of animals from different contemporary groups as we do with BLUP EBV's. Index values do not tell us anything about animals in different contemporary groups. However, since *i* and σ_H do not depend on which index is used for selection, maximum r_{IH} is obtained at any index scale. Thus, it is possible to standardize indexes to a common mean and variance, for example, to a mean 100 and SD 10 (or CV = 10%). This is easily done by converting the original index Ito the standardized index $I^* = (I - I) \times 10/\sigma_I + 100$, where I is the average original index and σ_l its SD. These indexes are still not comparable between contemporary groups but give a comparable indication on the relative genetic merit of individuals in different contemporary groups. Animals with index 110 in different contemporary groups are one SD above their respective means.

Performance recording *SWT* is key for both Abergelle and Bonga programmes. In the case of Abergelle programmes, recording dams *ADM* contribute substantially to gains, much more so if repeated average daily milk yields are available. In the case of Bonga programmes recording *NOB* is also recommended. Records from dams are necessary in programmes interested in restricting genetic gains

in NOB and AWT. Sometimes dam information is not available, for example when dams are not tagged or, in the case of dairy breeds, when systematic milk recording is too problematic. In that case, average daily growth between birth and 30 days may be used as a proxy for the dam's milk production, assuming the growing kid or lamb feeds exclusively on the milk of his mother. In Bonga programmes a selection candidate's own birth type (single or multiple) is equivalent to one record of dNOB and this information can be included in the index. Selection on such an index (not shown in the Tables) would add \$0.33 to the economic gain of \$3.22 obtained from selection on Index1B, very close to the \$\$3.60 obtained with selection on Index2B. Thus, using candidates own birth type records together with SWT in Bonga selection programmes achieves almost the same gains as when including dam records of NOB and s1. These recommendations most probably apply to comparable breeds in Ethiopia and other countries. For example, the recommendations for Bonga may apply also to the Doyogena and Horro sheep breeds and the recommendations for Abergelle may also apply to some extent to the Begavit goat breed.

No matter how detailed the breeding objective is defined and how comprehensive the available measurements included in the index, there will be most certainly farmer goal traits not formally considered or goal traits very weakly targeted through measurements. Such traits will need to be considered visually in addition to the formal selection on aggregate breeding objective. Farmer's interests will be for improvement of future generations but also for improvement of the current generation by culling animals with nonheritable, but permanent defects. Ignoring these traits may lead to less commitment of the farmers vis-à-vis the breeding programme. The room for visual selection should be inversely related to the accuracy of the selection index and completeness of breeding objective function. For example, the room for visual selection shall be small if a selection index is highly correlated with a breeding objective including most traits of interest, and shall be large if a selection index is lowly correlated with an incomplete breeding objective function.

In practice there will be an independent culling instance on preponderant traits such as coat colour and/or horn/tail type which may take place before any measurement is taken. Amongst the remaining candidates, it is recommended to first select on measured performance before final visual selection, for example, by selecting sires with above average indexes and then on appearance and other traits not considered in the objective function and measurements as implemented in Argentina's Merino sheep programme (AACM, 2020) or as suggested for nucleus males for distribution in Ethiopian communities (Gizaw et al., 2011). Such a procedure secures a positive selection differential on economically important traits while considering farmer's knowledge and particular interests.

Conclusions

Breeding objective functions for tropical goat and sheep populations were derived and evaluated in selection programmes based on different indexes. Sires in dual-purpose goat community breeding programmes should be selected on indexes including at least own early live weight and their dams average milk production records. Sires for meat sheep programmes should be selected on own early live weight and desirably also on their dam's number of offspring born. Restricting genetic changes in number of offspring born or adult weight is not recommended.

Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.animal.2021.100198.

Ethics approval

Not applicable.

Data and model availability statement

None of the data were deposited in an official repository. The software developed for this study is available upon request.

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Declaration of interest

None.

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